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## *Bairdemys*, a New Side-Necked Turtle (Pelomedusoides: Podocnemididae) from the Miocene of the Caribbean

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### ABSTRACT

A new genus, *Bairdemys*, is erected for two species of side-necked turtles. *Bairdemys venezuelensis* (Wood and Díaz de Gamero, 1971) from the late Miocene Urumaco Formation of Venezuela is represented by four skulls and a number of shells. *Bairdemys hartsteini* from the Miocene of Puerto Rico is known from a skull. *Bairdemys* is a member of the Podocnemididae because it possesses a cavum pterygoideus, and is related to the *Shweboemys* Group because it has a well-developed secondary palate. It differs from all other Podocnemididae in having large ventral convexities on the secondary palate, the eustachian tube separated by bone from the fenestra postotica, and the frontal and prefrontal strongly convex dorsally.

### INTRODUCTION

When Wood and Díaz de Gamero (1971) described *Podocnemis venezuelensis*, they assigned it to *Podocnemis* with a caution that if associated skull material were discovered it might require a different generic assignment. That skull material was discovered by Wood and others on a Harvard expedition to Venezuela in 1972, and it showed that *P. venezuelensis* was quite distinct from other spe-

cies assigned to *Podocnemis*. Another similar skull discovered in Puerto Rico by Eugene Hartstein shows close similarities to *P. venezuelensis*. As part of a revision of the Podocnemididae being undertaken by Gaffney, Wood, and our associates Drs. Peter Meylan and Haiyan Tong, we have concluded that a new genus should be named for these taxa. It is the purpose of this paper to diagnose and name these new taxa and provide brief

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descriptions based on the current literature. A more extensive comparative description involving the other Podocnemididae is under way.

We use the systematic terminology for pleurodires previously developed in Broin (1988), Antunes and Broin (1988), and more recently in Meylan (1996), Lapparent de Broin and Werner (1998), Gaffney et al. (1998), and Gaffney et al. (2001). This usage places the families Bothremydidae, Podocnemididae, and Pelomedusidae (restricted to *Pelusios* and *Pelomedusa*) in the Pelomedusoides (which equals the Pelomedusidae in the classic sense). A useful review of the pelomedusoid literature is Broin (1988). The only computer-generated cladogram of Podocnemididae available at present is Meylan (1996), which shows the relationships of these families and the included genera. The cranial description in this paper follows Gaffney (1979) which should be seen for a review of turtle skull morphology and an introduction to the relevant literature. *Bairdemys* is a member of the B9 taxon of Gaffney and Meylan (1988) and the “groupe *Schweboemys* [sic]” of Broin (1988). The content of this group as recognized here is listed below.

The new specimens of *Bairdemys venezuelensis* were collected by a 1972 Harvard–National Science Foundation expedition to Venezuela, consisting of Bryan Patterson, Arnold Lewis, Daniel Fisher, Robert Repenning, Michael Stanford, and Roger Wood. The fieldwork was done with the cooperation of the Escuela Geología y Minas, Universidad Central de Venezuela, and the Ministerio de Minas y Hidrocarburos. Four skulls, three lower jaws, and more than ten shells of *Bairdemys venezuelensis* were collected from one site, Turtle Hollow (fig. 1). Other fossil turtles from the Urumaco Formation collected by this expedition are *Stupendemys* (Wood, 1976a), a trionychid (Wood and Patterson, 1973), *Chelus* (Wood, 1976b; Sánchez-Villagra et al., 1995), and a testudinid (MC-MCZ, field number 159–72V). The Urumaco Formation is described in Díaz de Gamero and Linares (1989) with maps, sections, and a faunal list. Other elements of the large Urumaco fauna are described in Pascual and Díaz de Gamero (1969), Medina (1976),

Bocquentin Villanueva and Buffetaut (1981), Bocquentin Villanueva (1984), Lundberg et al. (1988), and Linares (1990). For more general paleobiogeographic information see Díaz de Gamero (1996), Kay and Madden (1997), and Iturralde-Vinent and MacPhee (1999).

#### Institutional Abbreviations

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum (formerly British Museum [Natural History]), London
MCNC	Museo de Ciencias, Caracas
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
VF	Escuela de Geología de la Facultad de Ingeniería de la Universidad Central de Venezuela, Caracas

#### Anatomical Abbreviations

bo	basioccipital
bs	basisphenoid
cp	cavum pterygoideus
ex	exoccipital
fr	frontal
ju	jugal
mx	maxilla
op	opisthotic
pa	parietal
pal	palatine
pf	prefrontal
pm	premaxilla
po	postorbital
pr	prootic
pt	pterygoid
qj	quadratojugal
qu	quadrate
so	supraoccipital
sq	squamosal

### SYSTEMATICS

ORDER TESTUDINES LINNAEUS, 1758

SUBORDER PLEURODIRA COPE, 1864

HYPERFAMILY PELOMEDUSOIDES COPE, 1868a

FAMILY PODOCNEMIDIDAE COPE, 1868b

***BAIRDEMYS*, new genus**

TYPE SPECIES: *Bairdemys hartsteini*, new species.



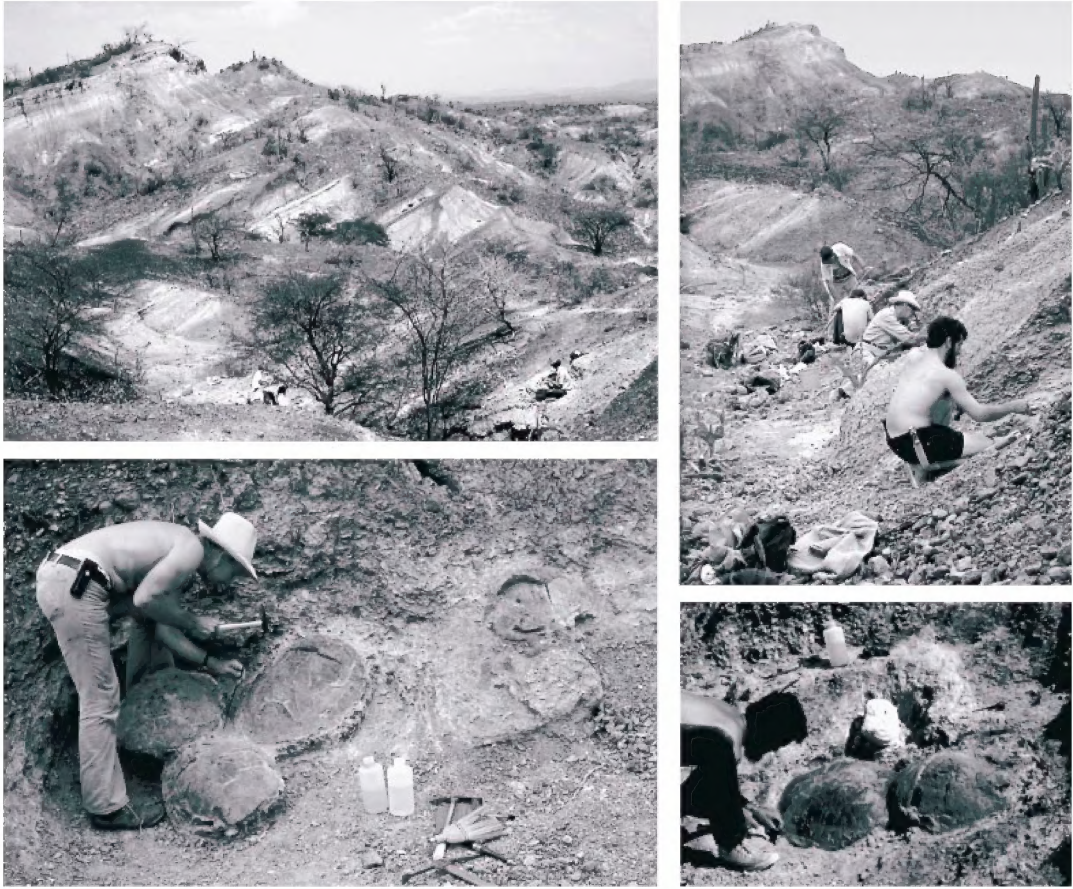


Fig. 1. Urumaco Formation, late Miocene, near Urumaco, Venezuela. Views of Turtle Hollow, the quarry that yielded the skulls of *Bairdemys* described here. **A**, General view of quarry area looking south; **B**, working the quarry face front to back: Dan Fisher, Bryan Patterson, Bob Repenning, Arnie Lewis; **C**, Arnie Lewis excavating shells of *Bairdemys venezuelensis*; **D**, Dan Fisher next to *Bairdemys venezuelensis* shells. The small white plaster jacket above the shells is one of the *Bairdemys* skulls. Photos taken by Roger Wood, Museum of Comparative Zoology expedition, Harvard University, 1972.

**DISTRIBUTION:** Miocene of Puerto Rico and Venezuela.

**DIAGNOSIS:** A *Shweboemys* Group *Pelomedusoides* (sensu Meylan, 1996) known from skull and shell; secondary palate shorter than in all *Shweboemys* Group except "*Shweboemys*" *gaffneyi*; medial edges of palatal cleft curved as in "*Shweboemys*" *gaffneyi*; ventral convexity on triturating surface larger than in all other *Shweboemys* Group; eustachian tube separated by bone from rest of fenestra postotica in contrast to all known Podocnemididae; antrum postoticum extremely small and slitlike in contrast to all other *Shweboemys* Group; frontal and

prefrontal strongly convex on dorsal surface in contrast to all other *Shweboemys* Group; basisphenoid separated from palatines by medially meeting pterygoids as in "*Shweboemys*" *antiqua*; basioccipital longer than in *Shweboemys pilgrimi*; jugal-ptyergoid contact prevents palatine-parietal contact.

**INCLUDED SPECIES:** *Bairdemys venezuelensis* (Wood and Díaz de Gamero, 1971), *Bairdemys hartsteini*, new species (see table 1 for comparisons).

**ETYMOLOGY:** The genus name is in honor of Dr. Donald Baird, a student of fossil turtles and other reptiles, who spent most of his career at Princeton University, and was an



TABLE 1  
Comparison of *Bairdemys* species

	<i>B. hartsteini</i>	<i>B. venezuelensis</i>
Snout shape	pinched	straight
Premaxillary notch	present	absent
Relative width of skull	narrower	wider
Palatal depressions	shallower	deeper
Skull size	smaller (80 mm)	larger (105–120 mm)

inspiring mentor of both authors. Don is active in many areas of vertebrate paleontology and fossil reptile research and has influenced many young people in paleontology. In 1964, when one of the authors, Gene Gaffney, was a senior at Rutgers University, Don was directly responsible for introducing Gene to fossil turtles. Roger Wood, the other author, as a Princeton undergraduate was also influenced by Don in entering paleontology.

*Bairdemys venezuelensis*  
(Wood and Díaz de Gamero, 1971),  
new combination

*Podocnemis venezuelensis*, Wood and Díaz de Gamero, 1971.

TYPE SPECIMEN: Laboratorio de Paleontología, Escuela de Geología de la Facultad de Ingeniería de la Universidad Central de Venezuela (Caracas), VF 1176, a complete carapace, figured by Wood and Díaz de Gamero (1971: plates 1, 2, 4).

TYPE LOCALITY: "... north of Campo El Mamon, state of Falcon, Venezuela" (Wood and Díaz de Gamero, 1971).

TYPE HORIZON: Capa de huesos/capa de tortugas, upper member of the Urumaco Formation, late Miocene (Díaz de Gamero and Linares, 1989).

DIAGNOSIS: A species of *Bairdemys* differing from the only other species, *Bairdemys hartsteini*, by having a straight rather than pinched snout, no premaxillary notch, a relatively wider skull, a more pronounced depression on the palatine surface of the palate, and a relatively larger skull (see tables 1, 2).

REFERRED SPECIMENS: VF 1173, plastron (figured in Wood and Díaz de Gamero, 1971:

plates 3, 4); VF 1174, plastron (figured in Wood and Díaz de Gamero, 1971: plate 5); VF 1177, carapace and plastron; VF 1177a, carapace and plastron; VF 1177b, partial shell; VF 1059, humerus. All presumably from same type locality and horizon (fide Wood and Díaz de Gamero, 1971). MCZ 9417 (field number 23–72V), nearly complete skull (figs. 6, 7) lacking only a portion of right temporal roof; MCNC-Pal-0001 (field number MCZ 21–72V), nearly complete skull (figs. 10, 11), slightly crushed and lacking portions of the braincase and palate; MCZ 9418 (field number 18–72V), skull (fig. 9) crushed mediolaterally; MC-Pal-0002 (field number MCZ 19–72V), skull (fig. 8) still embedded in matrix with ventral surface exposed; MC-MCZ 22–72V, lower jaws; MC-MCZ-26A-72V, lower jaws; MC-MCZ 21A–72V, lower jaws.

DISCUSSION: The new skulls described here were found in close proximity to shells of "*Podocnemis*" *venezuelensis* by the MCZ expedition in 1972. Although none were found in articulation with a shell and cervicals as a single individual, the consistent association of the skulls and shells (as seen in fig. 1D) leads us to conclude that they belong to the same species. The shell of "*Podocnemis*" *venezuelensis* is described in Wood and Díaz de Gamero (1971).

*Bairdemys hartsteini*, new species

TYPE SPECIMEN: AMNH 27222, a nearly complete skull (figs. 12–15). Collected by Eugene F. Hartstein, 1975.

TYPE LOCALITY: North side of Highway No. 2, west of Bayamon, Puerto Rico. See MacPhee and Wyss (1990: 37) for a more detailed description of this site.

TYPE HORIZON: Cibao Formation, middle Miocene. Nearby locality has manatee ribs, turtle shell, shark teeth, porpoise vertebrae (fide E. Hartstein, personal commun.). See MacPhee and Wyss (1990) for discussion of the Cibao Formation, its dating, and a general context of Puerto Rican Tertiary vertebrates.

DIAGNOSIS: A species of *Bairdemys* differing from the only other species, *Bairdemys venezuelensis*, by having a pinched rather

TABLE 2  
Measurements of the Skulls of *Bairdemys* (in mm)

	MCNC- Pal-0001	MCZ 9417	MCZ 9418	MCNC- Pal-0002	AMNH 27222
A. Midline length as preserved	121.0	105.0	72.4 <sup>a</sup>	96.0 <sup>a</sup>	80.3
B. Maximum width	106.5	106.5	64.0 <sup>b</sup>	95.0	74.7
C. Width between orbits	26.5	27.6	23.5	—	20.7
D1. Width of left orbit	31.1	27.9	24.0 <sup>a</sup>	26.4	21.0 <sup>b</sup>
D2. Width of right orbit	35.0	29.4 <sup>b</sup>	—	—	—
E. Width of external nares	22.2	19.7	—	23.0 <sup>a</sup>	12.9
F. Width of internal nares	8.9	4.2	—	7.0 <sup>a</sup>	3.8 <sup>b</sup>
G. Maximum height at quadrate	69.5	63.8	61.6	—	50.1
H. Width of skull at middle of orbits	63.9	65.0 <sup>b</sup>	—	50.0	44.0
I. Length from anterior margin of prefrontals to posterior margin of parietals	119.3	110.2	101.5 <sup>a</sup>	128.0 <sup>a</sup>	92.8 <sup>b</sup>
J1. Height of left orbit	21.4	22.5	—	12.0 <sup>a</sup>	19.3 <sup>a</sup>
J2. Height of right orbit	19.2	22.5	21.2	—	17.5
K. Skull height at occipital condyle	44.7	41.3	42.6	26.0 <sup>a</sup>	35.0
L. Anterior width of triturating surface	25.3 (L), 24.8 (R)	23.4	16.3	—	16.3 (L), 16.7 (R)
M. Posterior width of triturating surface	29.7 (L), 27.1 (R)	35.3	26.9	24.3 (L), 26.0 (R)	23.1 (L)
N. Width of palate across foramina palatinum posterius	46.5	47.2	—	43.0	33.5 <sup>b</sup>
O. Length from front of skull to posterior edge of condylus articularis	104.4	102.0	97.2	95.0	68.0

<sup>a</sup> Damaged.

<sup>b</sup> Estimated.

than straight snout, a premaxillary notch, a relatively narrower skull, a less pronounced depression on palatine surface of palate, and a relatively smaller skull (see tables 1, 2).

ETYMOLOGY: For Eugene F. Hartstein, who collected the specimen and donated it to the AMNH in 1991.

#### *Bairdemys*, species indeterminate

SPECIMEN: AMNH 30000, poorly preserved skull, figured in Sánchez-Villagra et al. (2000).

LOCALITY: Cerro La Cruz, NW area of Lara State, 4 km NW of Caserío La Mesa. See Sánchez-Villagra et al., 2000, for map.

HORIZON: Castillo Formation, early Miocene.

DISCUSSION: This skull was figured and briefly described in Sánchez-Villagra et al. (2000) as “genus indet., of ‘*Podocnemis*’ venezuelensis Wood and Díaz de Gamero, 1971”. The skull is clearly a *Shweboemys* Group podocnemidid based on its cavum pterygoideus and secondary palate. It has the palatal convexity diagnostic of *Bairdemys*. However, the skull differs from both species of *Bairdemys* in being flatter and lacking the degree of snout arching seen in *Bairdemys*. AMNH 30000 is not well preserved and these differences might be due to crushing, although there is no other indication of this. Unfortunately, sutures are not visible, and most of the bone surface is eroded.

Comparison with the diagnostic criteria of

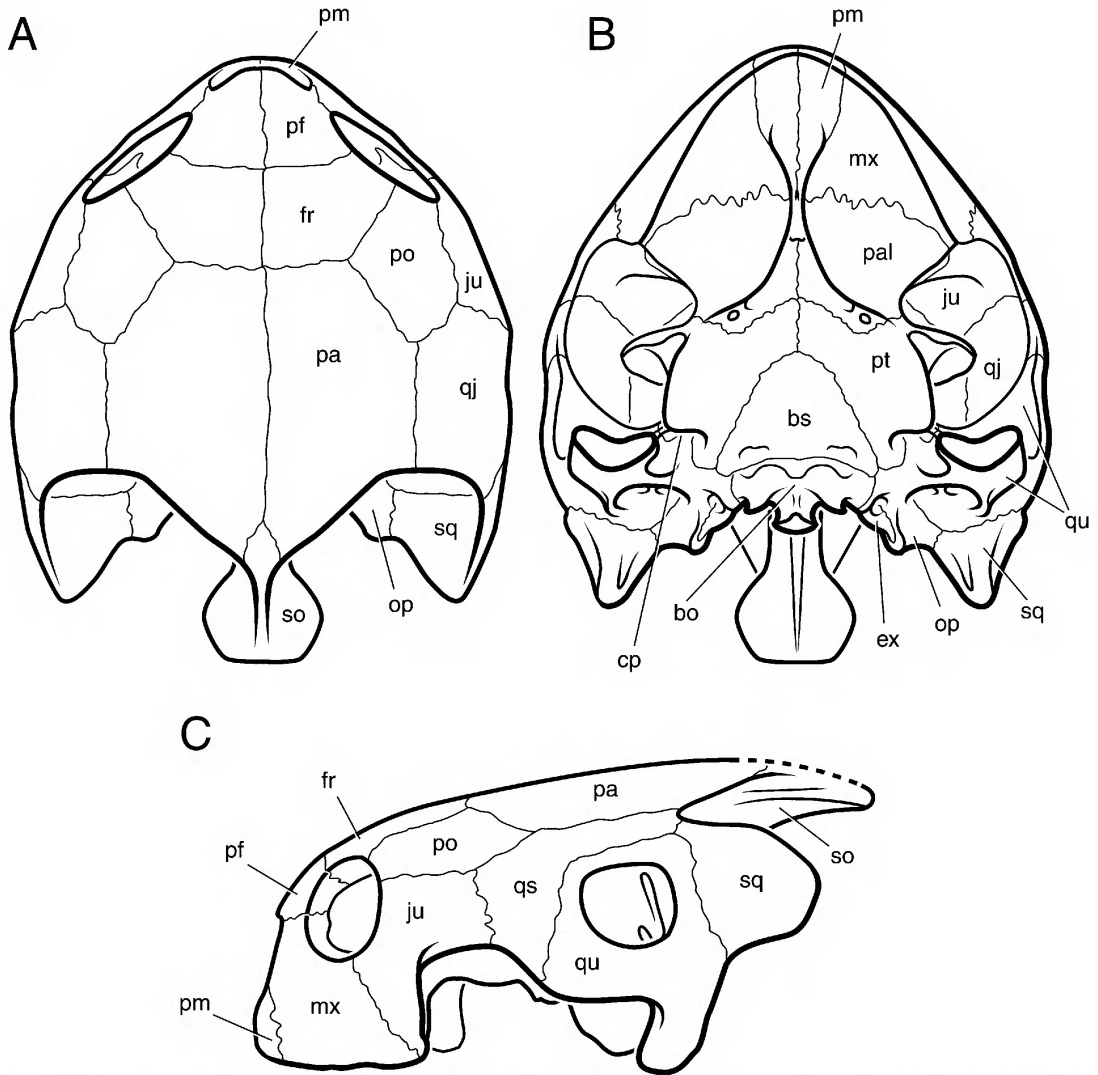


Fig. 2. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, skull reconstruction based primarily on MCZ 9417 with additions from MCZ 9418, MCNC-Pal-0002, and MCNC-Pal-0001. **A**, dorsal; **B**, ventral; **C**, lateral.

the *Bairdemys* species (table 1) shows that it has the straight rather than pinched snout of *B. venezuelensis*, and the apparently narrower skull and shallower palatal depressions of *B. hartsteini*. Its length is 92 mm, just intermediate between the 80 mm of *B. hartsteini* and the 105–120 mm of *B. venezuelensis*. AMNH 30000 could very well be a distinct species of *Bairdemys*, but its poor preservation makes it very difficult to be sure about the characters mentioned. For the present, we

leave it as an indeterminate species in *Bairdemys*.

#### COMPARED TAXA

In Gaffney and Meylan (1988), Broin (1988), and Meylan (1996), *Stereogenys* Andrews, 1901, and *Shweboemys* Swinton, 1939, are united among Podocnemididae by the unique possession of a secondary palate. This is the *Shweboemys* Group as recognized



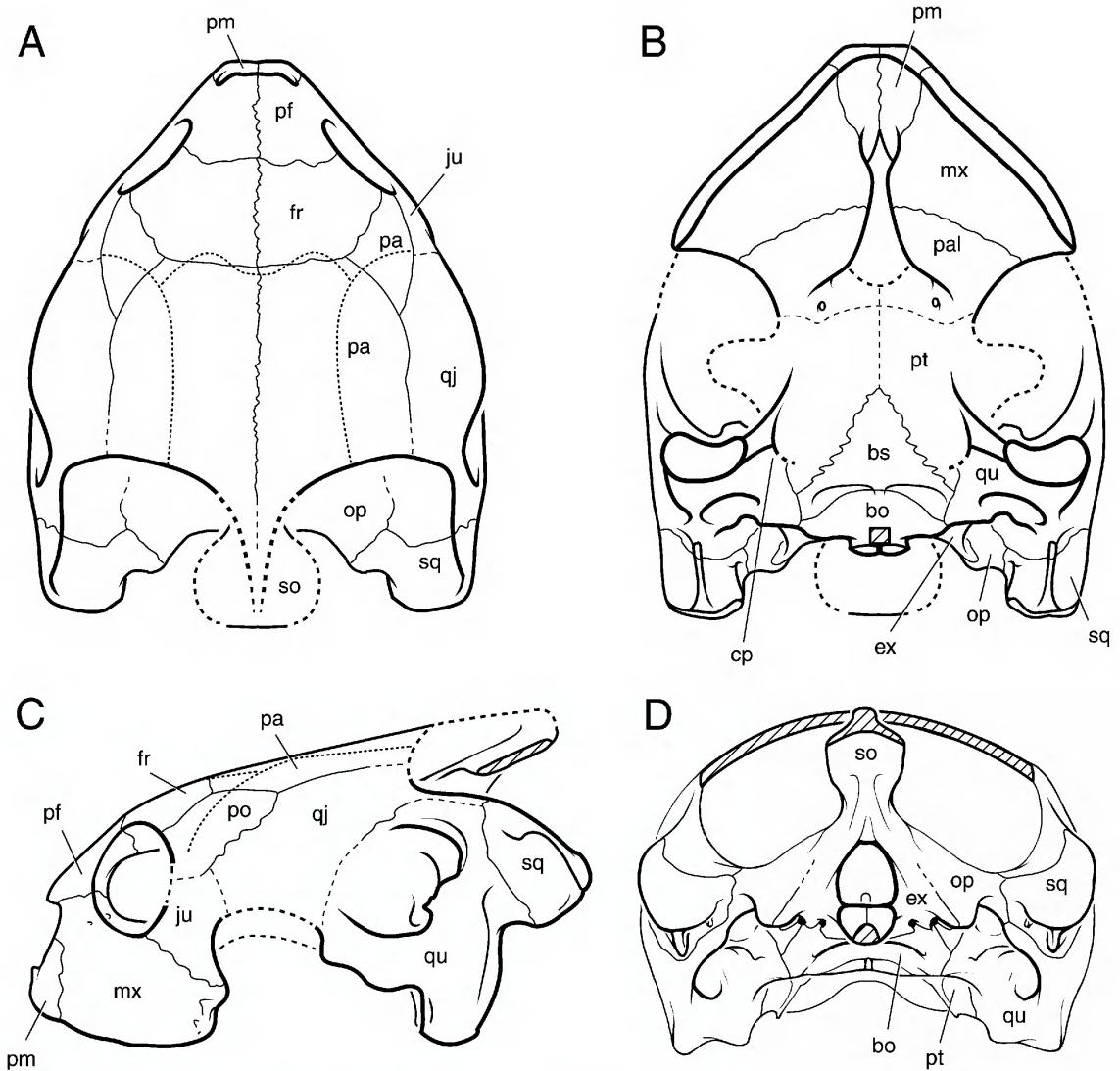


Fig. 3. *Bairdemys hartsteini*, new genus and species, skull reconstruction based entirely on AMNH 27222. **A**, dorsal; **B**, ventral; **C**, lateral; **D**, occipital.

here. Recent work on these and as yet undescribed close relatives suggests that the genus *Shweboemys* as currently recognized is not monophyletic. Therefore, we are indicating the specific taxa used in the *Bairdemys* description:

*Stereogenys cromeri* Andrews, 1901.

DISTRIBUTION: Late Eocene, Egypt.

AVAILABLE MATERIAL: Cairo Geological Museum C. 10027 (holotype), Cairo Geological Museum C. 1003, BMNH R.3190,

BMNH R.3189, BMNH R.3191, Duke Primate Center No. 4120.

LITERATURE: In addition to Andrews (1901), there is Andrews (1906), and von Reinach (1903: plate XI, fig. 2).

*Shweboemys pilgrimi* Swinton, 1939 (non *Schweboemys* de Broin 1988).

DISTRIBUTION: Burma, Pliocene (possibly Pleistocene).

AVAILABLE MATERIAL: Geological Survey of India No. 17255 (holotype figures in

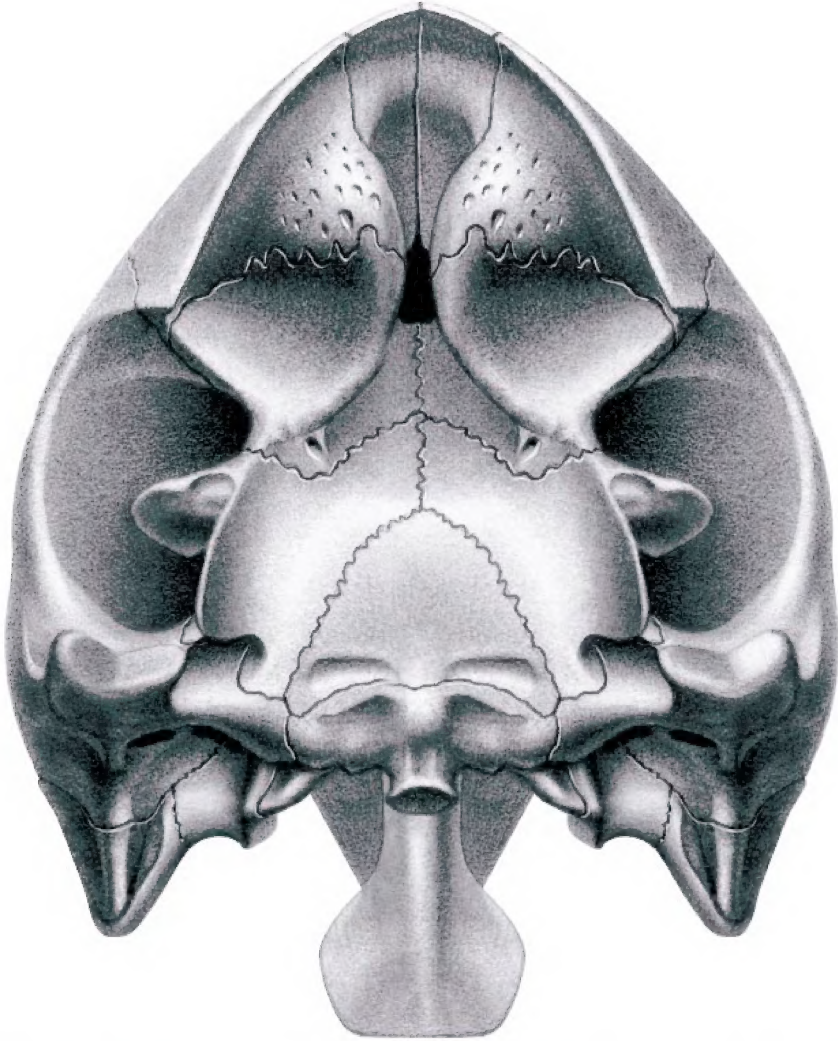


Fig. 4. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, reconstructed ventral view based primarily on MCZ 9417 with additions from MCZ 9418, MCNC-Pal-0001, and MCNC-Pal-0002. See figure 2 for labels.

Swinton, 1939: figs. 1, 2; and Wood, 1970: plate 1), BMNH R.8432 (figured in Wood, 1970: figs. 1, 2, 3, and plates IIA, IIIA, IVA).

LITERATURE: In addition to Swinton (1939), Wood (1970) provided description and figures.

*"Shweboemys" gaffneyi* Wood, 1970.

DISTRIBUTION: Pakistan, Miocene.

AVAILABLE MATERIAL: BMNH R.8570 (holotype, figured in Wood 1970: figs. 1, 2, and plates IIB, IIIB, IVB).

LITERATURE: Only described in Wood (1970).

*"Shweboemys" antiqua* Andrews, 1903.

DISTRIBUTION: Late Eocene, Egypt.

AVAILABLE MATERIAL: Yale Peabody Museum 6205 (figured in Gaffney, 1979: figs. 136, 137).

Jain (1977) described *Carteremys pisdurensis*, later (1986) referring the species to *Shweboemys*. We have not seen this material and have been unable to include it in our





Fig. 5. *Bairdemys hartsteini*, new genus and species, reconstructed ventral view of AMNH 27222. See figure 3 for labels.

podocnemidid revision yet. Although it has a broad maxillary triturating surface, it does not appear to have the secondary palate and narrow cleft of other *Shweboemys* Group taxa, and we have excluded it from our comparisons of *Bairdemys*.

#### DESCRIPTION

The best preserved skull of *Bairdemys venezuelensis*, MCZ 9417, is figured in more detail than the other specimens of this species. The single skull of *Bairdemys hartsteini* is figured in stereophotographs because it is particularly well preserved, and despite some breakage, reveals internal features that are useful in comparison with other podocnem-

idids. Measurements of the skulls are shown in table 2.

#### PREFRONTAL

Both right and left prefrontals are preserved in *Bairdemys hartsteini*. The prefrontal is present in all four *Bairdemys venezuelensis* skulls, but it is best preserved in MCZ 9417 and MCZ 9418. In MCNC-Pal-0001 it is damaged and concave dorsally rather than convex. In MCNC-Pal-0002 only the ventral surface is visible. The prefrontal is similar in *Bairdemys*, *Shweboemys*, and *Stereogenys*, forming the dorsal margin of the apertura narium externa and the anterior region of the skull roof between the orbits. As in other Pe-

lomedusoides, nasal bones are absent, the anterior margin of the prefrontals is a natural edge. The prefrontals slightly overhang the apertura narium externa in both species of *Bairdemys*.

In *Bairdemys* there is a transverse suture posteriorly with the frontal, and posterolaterally the prefrontal forms part of the orbital margin. Anteroventrally the prefrontal meets the dorsal process of the maxilla as in other *Pelomedusoides*. As in other pleurodires the ventral surface of the prefrontal bears a ridge separating the fossa orbitalis laterally from the sulcus olfactorius medially. The prefrontal in *Bairdemys* is a relatively broad bone, in contrast to the narrower prefrontal seen in *Podocnemis*.

#### FRONTAL

Both frontals are preserved in *Bairdemys hartsteini* and are complete except for small broken edges along the ventral margins. The frontal in *Bairdemys venezuelensis* is best preserved in MCZ 9417; both MCNC-Pal-0001 and MCZ 9418 show it clearly, but have some breakage. Only the ventral surface is visible in MCNC-Pal-0002, although a prominent skull roofing bone, the frontal in *Bairdemys*, is relatively thick with a strong ventral, parasagittal ridge. The frontal as exposed in the skull roof of *Bairdemys* contacts the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. The frontal forms the posteromedial margin of the orbit.

In lateral view the prefrontal and frontal of *Bairdemys* are dorsally convex, curving anteroventrally from the fronto-parietal suture. In *Stereogenys* and *Shweboemys* the skull roof is nearly flat in profile. *Podocnemis* approaches the degree of curvature in *Bairdemys*, but does not reach it.

The ventral surface of the frontal in *Bairdemys* is dominated by a thick and well-developed parasagittal ridge separating the fossa orbitalis laterally from the sulcus olfactorius medially. This ridge is lowest anteriorly where it is a continuation of the ridge on the ventral surface of the prefrontal that separates the fossa orbitalis and the fossa nasalis. The ridge on the frontal thickens and deepens posteriorly where it contacts the processus

inferior parietalis posteromedially and the posterior wall of the fossa orbitalis posterolaterally.

#### PARIETAL

Large portions of both parietals are preserved in *Bairdemys hartsteini*, but on both sides the posterior edges are missing. The left parietal is more complete than the right and it shows most of the lateral margin. On the ventral surface only the anterior part of the processus inferior parietalis is preserved on either parietal. The thickened medial edge of each parietal is preserved, but only an eroded surface represents the supraoccipital contact surface. As reconstructed, however, it appears that very little of the sutural contact with the supraoccipital is actually missing. The parietal is present in all four *Bairdemys venezuelensis* skulls, but is not complete in any. MCZ 9417 (left) and MCNC-Pal-0001 (left and right) show the dorsal plate best with clear sutures and only slight breakage. In MCZ 9418 most of the left parietal is present. In MCNC-Pal-0002 only a very small part of the ventral surface is visible.

The skull roof portion of the parietal in *Bairdemys* contacts the frontal anteriorly, the postorbital anterolaterally, the quadratojugal laterally, and the other parietal medially, as in the other *Podocnemididae*. The ventral surface of the parietal in *Bairdemys*, *Stereogenys*, and *Shweboemys* has a thick parasagittal, ventral ridge, the processus inferior parietalis, which forms the side wall to the cavum cranii. The anterior part of this ridge is nearly complete on both parietals in *Bairdemys hartsteini*, but posteriorly most of it is broken close to the temporal roof.

In the "Podocnemine Group" (B8 of Gaffney and Meylan, 1988) there is a variably developed bony wall behind the fossa orbitalis, separating it from the fossa temporalis. The dorsal part of this wall is formed by a ventral process of the postorbital laterally and by a ventrolateral process of the parietal medially. In *Bairdemys hartsteini* the ventral part of the wall is largely missing due to damage, but the dorsal portion is preserved and clearly shows that the wall was well developed. The parietal portion of the wall is thickest medially and thins laterally



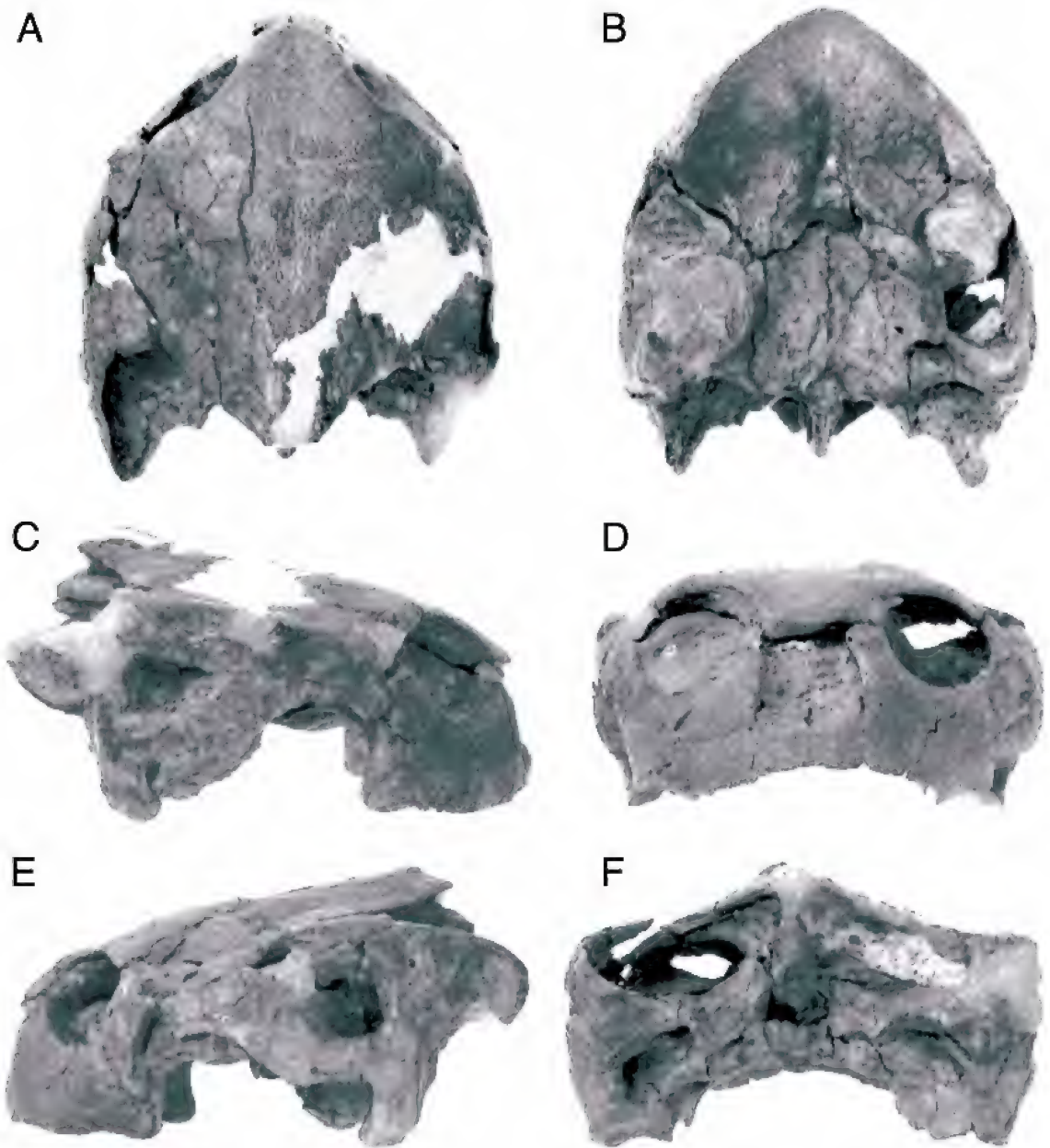


Fig. 6. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, MCZ 9417. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior.

to meet a similar sized postorbital flange. This parietal part of the wall behind the orbit is a lateral outgrowth of the processus inferior parietalis.

Ventrally the processus inferior parietalis

meets a thickened dorsal process of the palatine. Because much of the jugal and adjacent parts of the postorbital are missing in AMNH 27222, this contact is exposed posteriorly. However, the same area is better pre-

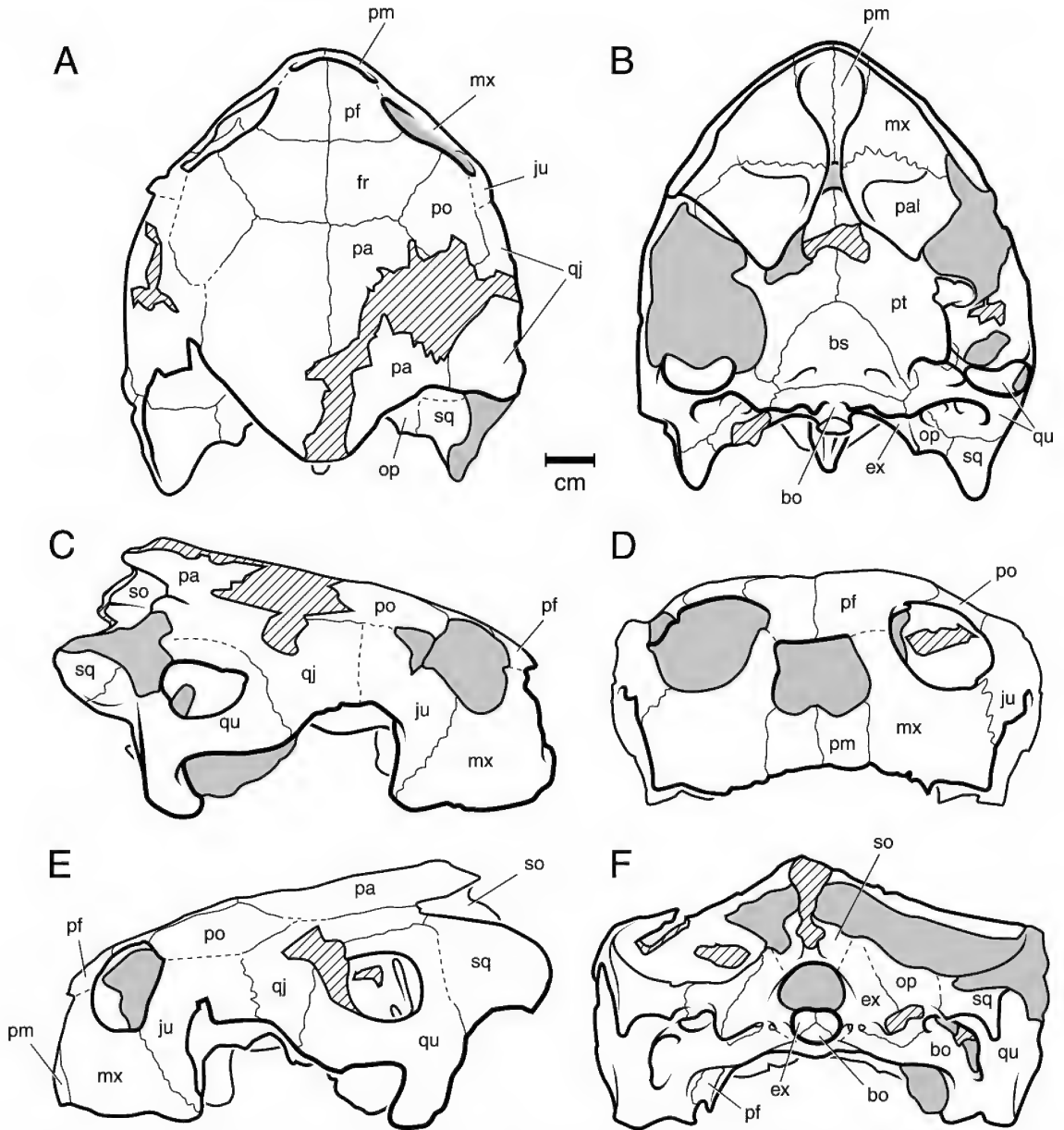


Fig. 7. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, MCZ 9417. Key to figure 6.

served in *Bairdemys venezuelensis* skulls, which show the contact covered externally by the jugal and postorbital processes. It is likely that this was the case in *Bairdemys hartsteini* as well. In *Shweboemys* and *Stereogenys* the dorsal process of the palatine is more extensive and is exposed in the post-orbital wall on the surface that faces the fos-

sa temporalis. *Podocnemis* completely lacks the parietal-palatine contact internally and externally. On the right side of *Bairdemys hartsteini* the processus inferior parietalis contacts a strong dorsal process of the pterygoid. In *Podocnemis* the pterygoid process is thinner and has a much narrower contact with the parietal.



In *Bairdemys* the two parietals overlies posteriorly the anterior part of the supraoccipital on the midline. The contact area is damaged on all three bones in AMNH 27222, and a tight sutural contact no longer exists. The relative position of the parietals and the supraoccipital is not definite and has been determined in the reconstructed skull by the agreement of other bones in the skull and by comparison with *Bairdemys venezuelensis*.

#### JUGAL

Parts of both jugals are preserved in *Bairdemys hartsteini*. The right jugal is almost entirely missing; only the dorsal part that contacts the postorbital externally is present. More of the left jugal is present, the ventral contact with the maxilla and part of the orbital margin. Between the two jugals the entire jugal portion of the orbital margin is known, but the posterior extent and medial contacts are missing. The jugal is preserved in all four *Bairdemys venezuelensis* skulls, but it is not complete in any. Clear sutures can be seen best in MCZ 9417 and MCZ 9418. The medial jugal process is not well preserved in any, but MCZ 9417 shows it best. In MCNC-Pal-0002 the jugal is visible in lateral and ventral views, but it is damaged.

The jugal of *Bairdemys* forms the posterioventral margin of the orbit between the postorbital and maxilla, as in all Pelomedusoids. The degree of exposure is less than in *Shweboemys*. The posterior limits of the jugal in *Bairdemys hartsteini* are not preserved and the contact with the quadratojugal is not known. *Bairdemys venezuelensis* has well-preserved cheek regions that show a distinctive semicircular emargination formed by the jugal anteriorly and quadratojugal posteriorly. This type of emargination is most similar to that seen in *Podocnemis*.

#### QUADRATOJUGAL

The left quadratojugal is preserved in *Bairdemys hartsteini*, but it lacks its posterior free margin and the area bordering the cheek emargination. The quadratojugal is present in all four *Bairdemys venezuelensis* skulls, but not complete in any. MCNC-Pal-0001 and MCZ 9417 show it best, but MCZ 9418 has

useful portions preserved. In MCNC-Pal-0002 only part of the lateral and internal surface can be seen.

The quadratojugal of *Bairdemys* contacts the jugal anteriorly, the postorbital antero-dorsally, the parietal medially, and the quadrate posteriorly. Above and posterior to the quadrate, a thin process of the quadratojugal contacts the squamosal. In these contacts *Bairdemys* agrees closely with all other Pelomedusoids except *Podocnemis*, which has a very small postorbital and lacks a quadratojugal-postorbital contact. As in nearly all other turtles the quadratojugal of *Bairdemys* has a curved contact with the quadrate paralleling the cavum tympani margin. The quadratojugal and the jugal form most of the edge of the cheek emargination in pelomedusids. In *Bairdemys hartsteini* most of this contact is missing. However, the surrounding bone that is preserved precludes a very extensive cheek emargination and is consistent with the degree seen in *Bairdemys venezuelensis*.

#### SQUAMOSAL

Most of both right and left squamosals are preserved in *Bairdemys hartsteini*, although the left one is more complete. The MCZ 9417, MCNC-Pal-0001, and MCZ 9418 skulls of *Bairdemys venezuelensis* have useful portions of the squamosal preserved, but none are complete. It is best preserved in MCZ 9417, but none have entirely clear sutures. In MCNC-Pal-0002 the bone is mostly missing.

As in all other turtles the squamosal of *Bairdemys* lies on the posterodorsal margin of the quadrate. It has a narrow contact with the quadratojugal anteriorly and forms the posterolateral margin of the temporal emargination. In all turtles the squamosal is the primary bone forming the outer cone-shaped covering of the antrum postoticum, which is a space behind and above the cavum tympani. In some pelomedusids, such as *Pelusios* and *Pelomedusa*, the antrum postoticum is relatively large, as in nearly all other turtles, but other Pelomedusoids have a variably reduced antrum postoticum. In most podocnemidids the antrum is smaller than in *Pelusios*, but is still a distinct space filling the

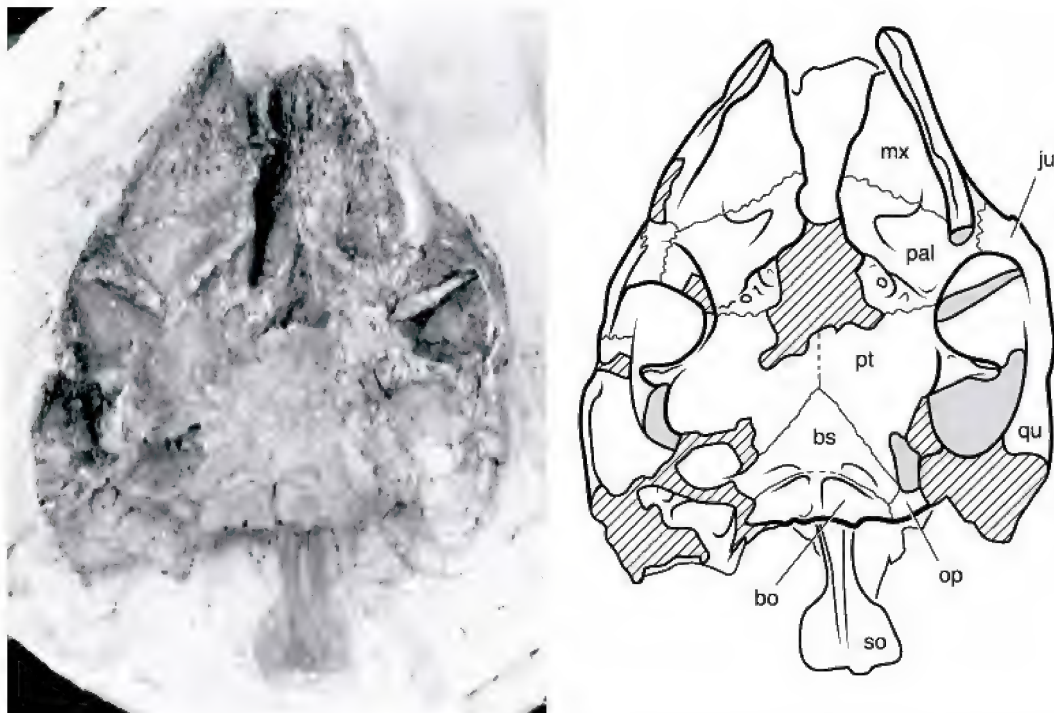


Fig. 8. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, MCNC-Pal-0002 in ventral view.

posterior projection of the squamosal. In *Bairdemys* and *Stereogenys* the antrum is reduced to a slit formed primarily by the quadrate internally and enclosed by the cone-shaped squamosal. The slit is orientated dorsolaterally-ventromedially. Both species of *Bairdemys* have a collapsed, slitlike antrum postoticum.

#### POSTORBITAL

Neither postorbital of AMNH 27222 is complete, but the posterior margins lacking in the right postorbital are preserved in the left one, so that nearly all of the bone is known. The postorbital is present in all four *Bairdemys venezuelensis* skulls, but is broken or damaged in all. The best preserved postorbital is on the right side of MCNC-Pal-0001. In MCNC-Pal-0002 only part of the ventral surface is visible.

The postorbital in *Bairdemys* is very similar in shape and size to that bone in "*Shweboemys*" *antiqua*, which is the one other species in the B9 taxon of Gaffney and Meylan (1988) that has the postorbital completely

known. The postorbital of *Bairdemys* contacts the frontal medially, the parietal posteromedially, the quadratojugal posterolaterally, and the jugal ventrally. The postorbital forms the posterodorsal margin of the orbit.

#### PREMAXILLA

The premaxilla is complete in *Bairdemys hartsteini*. The premaxilla in *Bairdemys venezuelensis* is present on both sides in MCZ 9417 and MCNC-Pal-0001, and on the left side of MCZ 9418. It is entirely missing in MCNC-Pal-0002.

In lateral view the premaxilla of *Bairdemys* has a nearly vertical contact with the maxilla posteriorly. In ventral view the premaxilla is a triangular element and contacts the maxilla posterolaterally. The premaxilla contacts the other premaxilla on the midline for its entire length. As a vomer is absent in *Bairdemys*, the only bone that the premaxilla is in contact with is the maxilla.

The premaxilla is an important element in the distinctive triturating surface morphology characteristic of *Bairdemys*, *Stereogenys*,



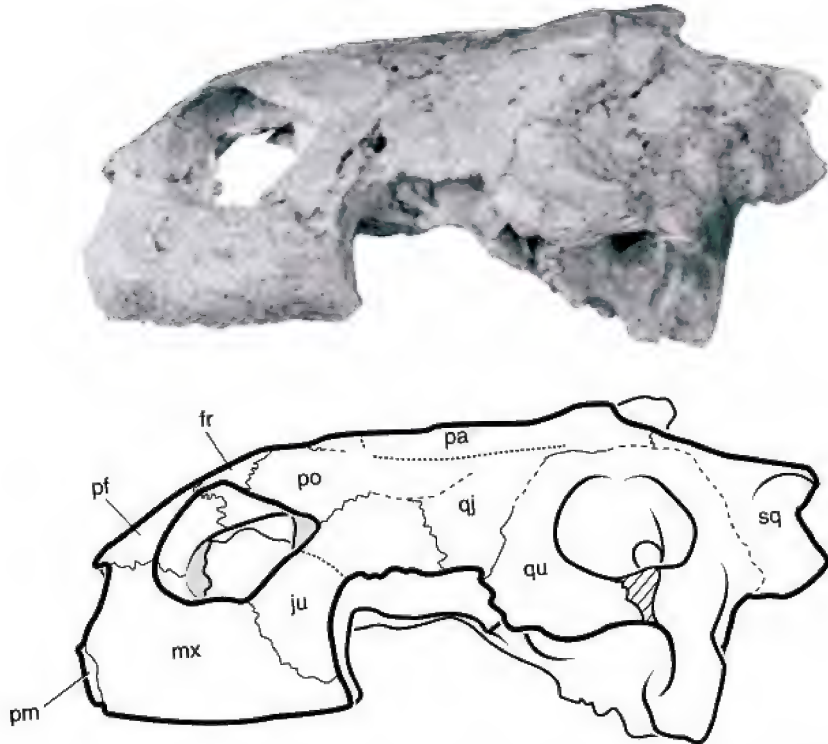


Fig. 9. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), new genus, MCZ 9418 in left lateral view.

*Shweboemys*, and the other species in the "Shweboemys" Group. All the members of this group have a secondary palate formed primarily from the maxilla and palatine. The premaxilla forms the anteromedian part of the triturating surface and the labial ridge that is the edge of the triturating surface. In *Bairdemys* the premaxillary surface forms a ventrally opening concavity on the midline. *Shweboemys* also has a median premaxillary depression, but is shallower and smoothly continuous with the posterolateral or maxillary surface of the triturating area. The premaxilla in *Bairdemys*, *Stereogenys*, and *Shweboemys* forms the anterior margin of the palatal cleft. The margin is a C-shaped trough, opening posteriorly. In *Podocnemis* and *Dacquemys* the maxillae meet behind the premaxillae, but in the other vomerless podocnemidids the premaxillae are free posteriorly.

The premaxillary portion of the snout shows varying degrees of protrusion or "pinching" in the *Bairdemys* species. *Bair-*

*demys hartsteini* is pinched and protruded, while *Shweboemys* is slightly protruded but not pinched. *Bairdemys venezuelensis* lacks pinching and a protrusion. Wood (1970) characterized "Shweboemys" *gaffneyi* as having a horizontal midline labial ridge and *Shweboemys pilgrimi* and "Shweboemys" *antiqua* as being notched on the midline in anterior view. Unfortunately, the two Asian species are represented by specimens that are broken in this area, but it does seem likely that at least *Shweboemys* has a premaxillary notch or embayment similar to that seen in *Bairdemys hartsteini*. *Bairdemys venezuelensis* lacks a notch. *Shweboemys antiqua* also has an embayment similar to that in *Bairdemys hartsteini*, and the partially preserved specimens of *Stereogenys* also seem consistent with a notch.

Dorsally the premaxilla forms the ventral margin and part of the lateral margin of the apertura narium externa. The oval apertura is similar in shape in both *Bairdemys* species. *Stereogenys* and *Shweboemys* are damaged in

this area, but show what appear to be broader narial openings. In *Bairdemys* there is a median, anteroposteriorly oriented ridge on the dorsal surface of the premaxilla that begins at the anteroventral margin of the apertura narium externa and rises in height along the floor of the fossa nasalis. There is a similar ridge in *Podocnemis*.

#### MAXILLA

The maxilla is complete in *Bairdemys hartsteini*. The maxilla is present in all four skulls of *Bairdemys venezuelensis*, but is best preserved in MCZ 9417. The skull of MCZ 9418 has a disarticulated maxilla showing internal features. Skulls MCNC-Pal-0001 and MCNC-Pal-0002 have maxillae preserved, but show some damage.

The contacts of the maxilla in *Bairdemys* are with the premaxilla anteromedially, the palatine posteriorly, the jugal posterodorsally, and the prefrontal anterodorsally. The maxilla forms part of the floor of the fossa orbitalis and bears a dorsal process that reaches the prefrontal. A parasagittal ridge, continuous with the base of that process, extends posteriorly and separates the orbital floor from the choanal groove, as in the other Pelomedusoides. A large foramen accompanied by a series of smaller, communicating foramina penetrates the maxilla in the orbital floor. This foramen is unidentified in Gaffney (1979: see fig. 54 and text) following Albrecht (1967, 1976). A similar series of foramina are in *Podocnemis*. More anteriorly, in the lateral wall of the choanal channel, is the foramen alveolare superius.

The vertical plate of the maxilla bears the labial ridge, the outermost part of the triturating surface. In *Bairdemys* the labial ridge is relatively deep and narrow. These are in contrast to the labial ridge of *Stereogenys*, which is lower and thicker. *Shweboemys*, *Stereogenys*, and *Bairdemys* have as their principal synapomorphy a well-developed secondary palate. Secondary palates occur in a number of other turtle groups, with *Erquellesia* and *Rhetecheys* (Gaffney 1979) having the most extensive. The *Shweboemys* Group, however, differs from all other turtles with secondary palates in having a midline cleft extending from the premaxillae poste-

riorly to the choanal opening proper. Was this cleft covered with soft tissue in life? Did the cleft provide an opening for air or other material? Did it mean that these turtles were warm-blooded?

The maxilla in the *Shweboemys* Group forms the anterolateral part of the palate and the palatine forms the posterior part. The maxilla-palatine suture trends laterally from the midline, then curves posterolaterally until it reaches the jugal in the margin of the fenestra temporalis inferior. In *Bairdemys* the maxillary part of the triturating surface has a distinct swelling or convexity just lateral to the midline cleft and internal to the labial ridge. This convexity is part of a raised platform that (in ventral view) is stepped above the palatine portion of the palate. The maxilla-palatine suture in *Bairdemys* intersects part of the convexity, but for the most part lies close to the demarcation between the anterolateral raised section and the more posterior lower section. *Shweboemys* and *Stereogenys* have much flatter, triturating surfaces; there is a gentle curve to the surface, but no raised convexity is present.

#### PALATINE

Most of both right and left palatines are preserved in *Bairdemys hartsteini*, but are damaged posteriorly along the jugal and pterygoid contacts and lack the dorsomedial part. The palatine of *Bairdemys venezuelensis* is present in all four skulls, but is best preserved in MCZ 9417 and MCZ 9418.

The palatine in *Bairdemys* is a relatively large and complex bone, with a horizontal plate forming the posterior portion of the secondary palate ventrally, a vertical plate extending dorsally to the parietal, and another horizontal plate meeting on the midline to form the primary palate. The presumed primitive condition of the palatine in turtles in general and Pelomedusoides in particular is a flat, platelike bone forming the roof of the palate, the posterior margin of the apertura narium interna, and a small anterolateral contribution to the triturating surface. In *Bairdemys* the palatine shows two modifications from this primitive condition: a secondary palatal plate ventral to the primary palatal palate, and a vertical process extending dor-



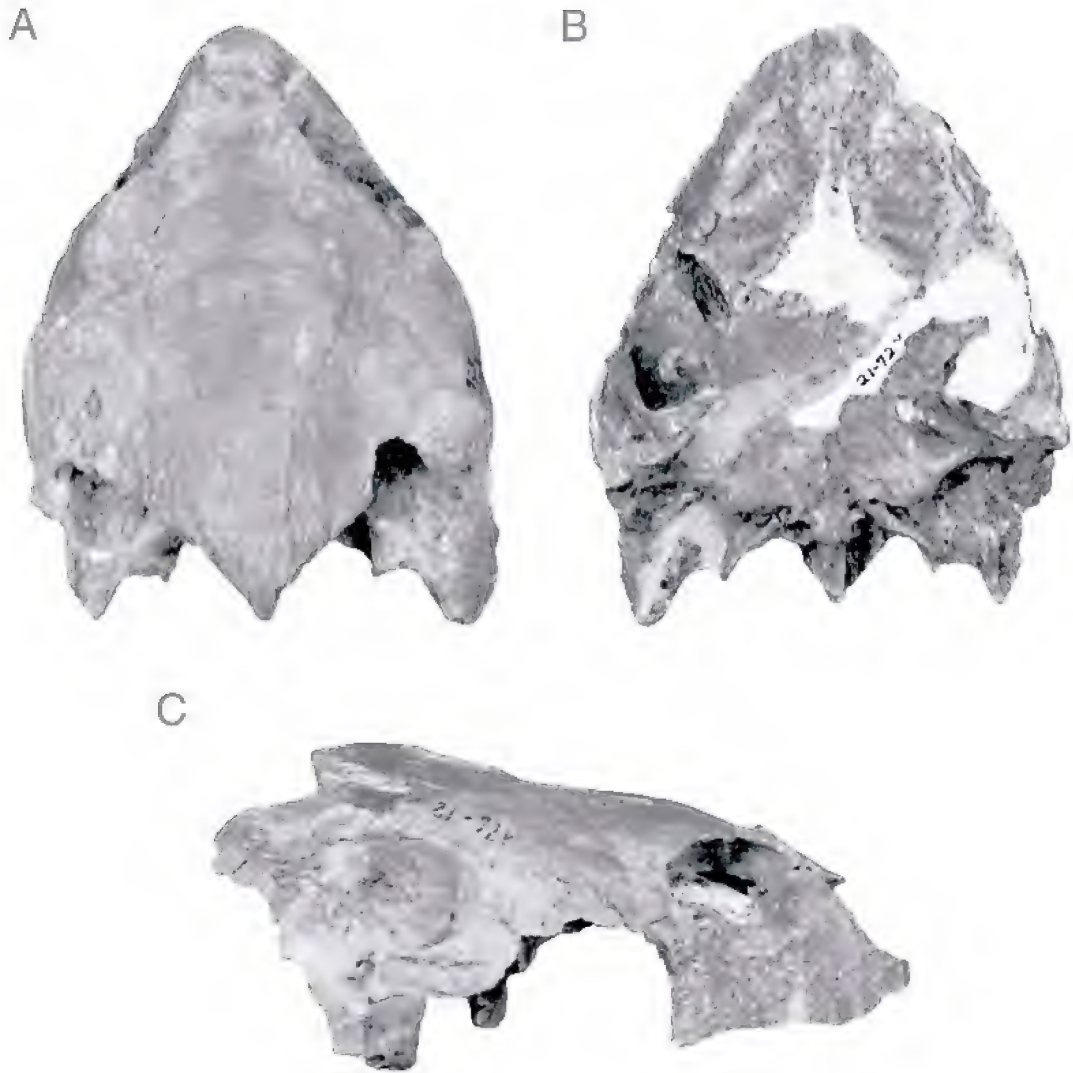


Fig. 10. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), MCNC-Pal-0001. **A**, dorsal; **B**, ventral; **C**, right lateral.

sally to the primary palate and the temporal roofing bones.

The primary palate portion of both palatines in *Bairdemys hartsteini* is broken, but shows the broken edge and the choanal tube formed between the primary palate and the secondary palate. The secondary palate of *Bairdemys* is formed by a broad plate ex-

tending posteriorly from the maxilla to reach the jugal posterolaterally in the margin of the fossa temporalis inferior and extending medially just short of the midline. A unique feature of the *Shweboemys* Group is the midline cleft formed by the premaxillae anteriorly and the maxilla and palatine laterally. Andrews (1906) described *Stereogenys* with the

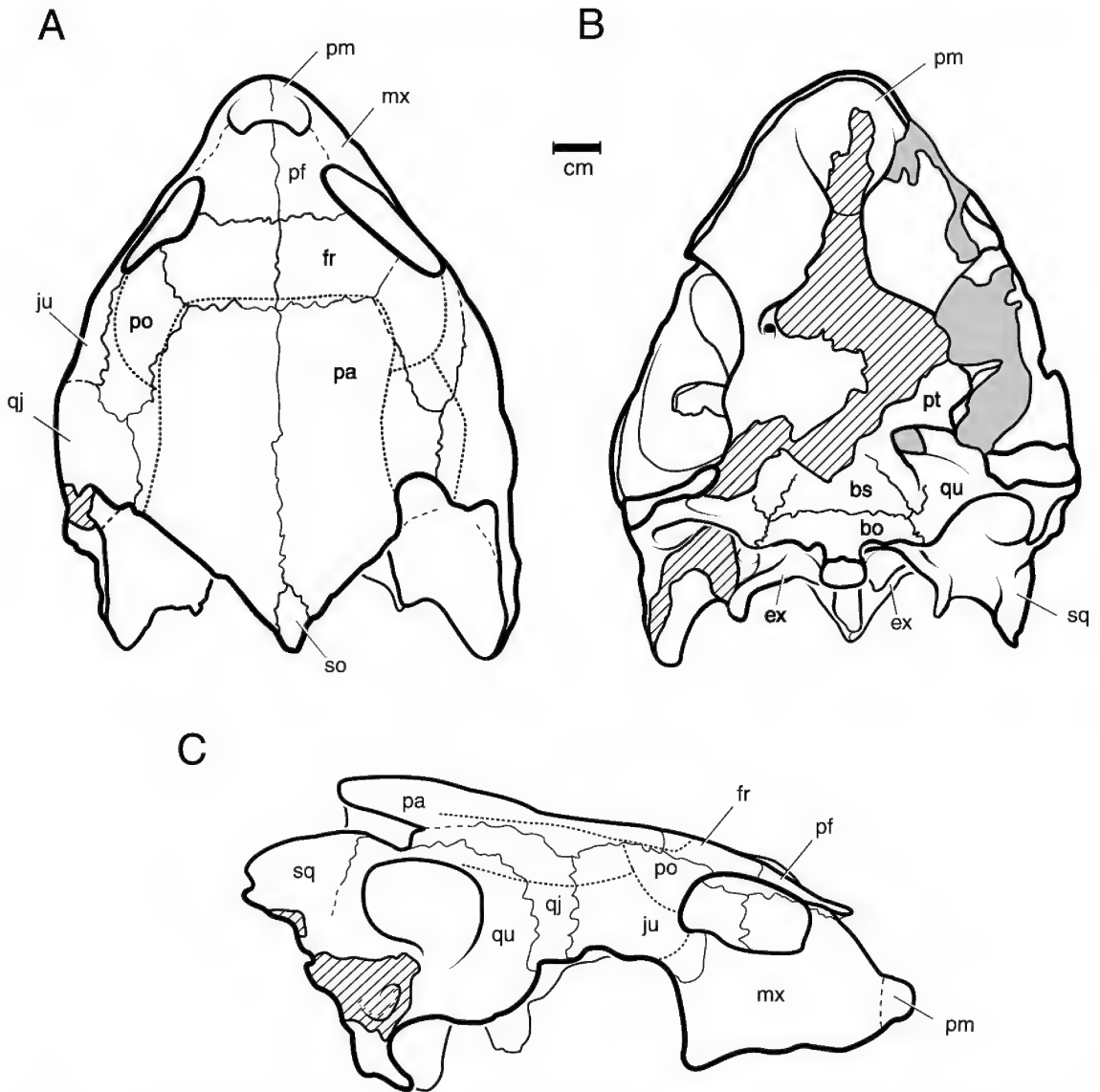


Fig. 11. *Bairdemys venezuelensis* (Wood and Díaz de Gamero), MCNC-Pal-0001. Key to figure 10.

palatines meeting on the midline, but this was an error of interpretation based on a laterally crushed skull, BMNH R3189. Three other skulls of *Stereogenys* that are not crushed laterally, Duke Primate Center 4120, BMNH R3190 and BMNH R3007 (cast), all show a midline cleft as in the other *Shweboemys* Group.

The extent of the secondary palate varies within the *Shweboemys* Group. The maxilla forms the anterior part of the secondary palate, less than one-third of the length, while

the palatine forms the posterior and dominant part. The variation in length of the secondary palate is mostly dependent on the palatine length and the degree of palatine participation. There is a range of variation in length of the secondary palate from *Stereogenys*, which has the longest secondary palate, to *Bairdemys*, which has the shortest.

A feature of the palatine used by Wood (1970) to differentiate *Shweboemys pilgrimi* from "*Shweboemys*" *gaffneyi* involves the margin of the palatal cleft. As preserved, the

cleft margins are parallel in *Shweboemys pilgrimi*, but in "*Shweboemys*" *gaffneyi* they diverge anteriorly and posteriorly. *Stereogenys* agrees with *Shweboemys pilgrimi* in having straight, parallel edges to the midline cleft, and they both differ from *Bairdemys* and "*Shweboemys*" *gaffneyi*, which have the palatal cleft edges diverging from each other, producing a curved edge.

The palatine in most turtles (e.g., *Chelydra*) is a relatively flat bone, but in many Pelomedusoides there is a dorsal process arising in the postorbital wall. In the living Pelomedusoides there is a distinct dorsal process of the palatine medial to the jugal and anterior to the pterygoid (Gaffney, 1979: figs. 53, 54). In the *Shweboemys* Group the process is unusually well developed, presumably as a support for the crushing palate, but its extent is hard to determine except in very well-preserved specimens. In *Bairdemys* the process extends dorsally to reach a ventral process of the parietal. The palatine-parietal contact is exposed only on the medial surface of the postorbital wall. On the other surfaces the palatine is covered by a postorbital-ptyergoid contact except in *Stereogenys* and *Shweboemys*, which have the dorsal palatine process exposed in lateral view. The dorsal process of the palatine is very prominent in the postorbital wall as seen within the fossa orbitalis, and forms a fissura ethmoidalis-like structure (see Frontal). In the postero-medial area of the fossa orbitalis the palatine process is a thick buttress that meets a short ventral ridge of the frontal. This buttress is the lateral wall of the sulcus palatinopertygoideus.

The sulcus palatinopertygoideus (Antunes and Broin, 1988: fig. 3) is formed between the side wall of the braincase proper, the parietal and pterygoid, and the processus trochlearis pertygoidei and its anterior palatine and jugal buttress. The sulcus is floored by the pterygoid posteriorly and the palatine anteriorly. Posteriorly the sulcus is open dorsally, but anteriorly it is closed over by the parietal and postorbital. In life the sulcus contains the pars rostro-medialis of the M. pertygoideus (Schumacher, 1973: figs. 9, 11). In *Pelusios* and *Pelomedusa* the sulcus palatinopertygoideus is relatively short, but in the Podocnemididae it is much longer. What appears to be the foramen palatinum poster-

ius is visible in *Bairdemys venezuelensis* only on the right side of MCNC-Pal-0001. This foramen seems to be very small or absent in the other *Shweboemys* Group taxa.

#### QUADRATE

Both right and left quadrates are preserved in *Bairdemys hartsteini*, but neither are complete. Both lack portions of the cavum tympani anteriorly, and the right quadrate lacks some of the medial portions. The quadrate of *Bairdemys venezuelensis* is not well preserved in any of the skulls, although they all have at least part of one present. Skulls MCZ 9417 and MCZ 9418 have the best quadrates, and with the right quadrate of MCNC-Pal-0001 provide a complete knowledge of the bone. Only fragments of the right quadrate remain in MCNC-Pal-0002.

Laterally the quadrate is the principal component of the cavum tympani. Some of the anterior parts of the cavum tympani are missing on both sides of *Bairdemys hartsteini*, but from the preserved areas, particularly on the left quadrate, it is likely that a precolumellar fossa of the sort seen in *Erymnochelys madagascariensis* and *Podocnemis unifilis* (Williams, 1954; Gaffney, 1979) is absent, as in *Podocnemis expansa*. There is no evidence of a precolumellar fossa in *Stereogenys*, and the area is not preserved in *Shweboemys*. The entrance into the antrum postoticum in *Bairdemys* is a narrow slit, roughly oriented dorsolateral-ventromedial. The antrum itself is very small, smaller than in any other *Shweboemys* Group. Although larger than in *Bairdemys*, the antrum postoticum of "*Shweboemys*" *antiqua* is significantly smaller than in other Podocnemididae. The antrum postoticum is indeterminate in *Shweboemys pilgrimi* and "*Shweboemys*" *gaffneyi*.

The incisura columellae auris in *Bairdemys* is completely surrounded by bone and encloses both the stapes and the eustachian tube. In all members of the *Shweboemys* Group with this area preserved, the bone surrounding the incisura posteriorly is much thicker than in other Podocnemididae, and in *Bairdemys* it is particularly extensive. On the right side of AMNH 27222 the dorsal part of the quadrate is broken, revealing the fenestra



ovalis and the passage connecting this with the incisura columellae auris. A posterior opening of this passage contained the eustachian tube, which exited on the posterior surface of the quadrate. The eustachian tube in most *Pelomedusoides* exits into the fenestra postotica along with the other structures, such as the stapedia artery and lateral head vein, normally found there (Gaffney, 1979). In both species of *Bairdemys* the eustachian tube is separated from the fenestra postotica, as well as the cavum acustico-jugulare, by a bony wall. In "*Shweboemys*" *antiqua* and *Stereogenys* it is absent; it is indeterminate in *Shweboemys pilgrimi* and "*Shweboemys*" *gaffneyi*. The condition does not occur in any other turtle.

On the lateral side of the skull, the quadrate contacts the quadratojugal anteriorly, beyond the edge of the cavum tympani. Most of the quadrate along this contact is missing in AMNH 27222, but its position can be determined by the matching sutural edge of the dorsal part of the quadratojugal preserved on the left side, and the ventral part of the quadrate preserved on the right side. Medial to the cheek the anterior surface of the quadrate in *Bairdemys hartsteini* is a vertical wall, slightly concave anteriorly, facing the adductor muscle chamber. This surface is usually inclined in chelids and vertical in *Pelomedusoides*. In both species of *Bairdemys* there is a narrow ridge or spine on the dorsal portion of the quadrate near the position in which the processus trochlearis oticum is found in cryptodires. The ridge trends dorsoventrally and slightly ventrolaterally. It begins on the more horizontal surface of the quadrate dorsally, where it is broken, so that its dorsal limits are not preserved. The bone making up the ridge is identical to the bone making up the surrounding parts of the quadrate and there is no indication that it bore or was associated with cartilage or a trochlea; rather, the ridge is more similar to structures associated with muscle or tendon attachment sites, although in this case its function is unknown.

The anteromedial corner of the quadrate meets the quadrate ramus of the pterygoid. The right quadrate of *Bairdemys hartsteini* lacks the pterygoid itself, but the sutural surface of the quadrate is preserved showing the

pterygoid contact. Posterior to the pterygoid the quadrate forms the dorsolateral wall of the large carotid canal, the cavum pterygoideus, characteristic of the Podocnemididae. This structure, named here for the first time formally, is described and figured in a number of podocnemid papers, but principally in Gaffney (1979), where it is termed the "pterygoideus muscle chamber" (e.g., figs. 84, 86), and in Schumacher (1973: fig. 11).

The medial contacts of the quadrate in *Bairdemys* are with the basisphenoid anteriorly and the basioccipital posteriorly on the ventral surface and with the opisthotic posteriorly and the prootic anteriorly on the dorsal surface. This is the condition in other Podocnemididae and pleurodires generally. The path of the stapedia artery can be seen in the left quadrate of *Bairdemys hartsteini*. It begins in the lateral margin of the fenestra postotica at the aditus canalis stapedio-temporalis, which, due to the subdivision of the fenestra postotica, is the prominent groove. The prootic portion of the canalis stapedio-temporalis is missing, but the quadrate forms the more lateral part of the canalis as it extends above the canal for the columella auris and curves anterodorsomedially toward the position of the foramen stapedio-temporale. The foramen stapedio-temporale is not preserved in AMNH 27222, but from what is preserved of the left quadrate and right prootic, the foramen appears to lie in the quadrate-prootic suture at the anterodorsal corner of the otic chamber as in the other *Shweboemys* Group taxa.

#### PTERYGOID

Only posterior and posteromedial parts of the pterygoid are preserved in *Bairdemys hartsteini*. The pterygoid is present in all four of the *Bairdemys venezuelensis* skulls, but the best one is the left side of MCZ 9417. The right side of MCNC-Pal-0001 has important areas preserved, and both MCZ 9418 and MCNC-Pal-0002 provide useful information on this bone.

The anteriormost parts preserved of the pterygoid in *Bairdemys hartsteini* do not show the midline, but the basisphenoid clearly has sutural surfaces ventrally that show the pterygoids met on the midline as in *Bairde-*

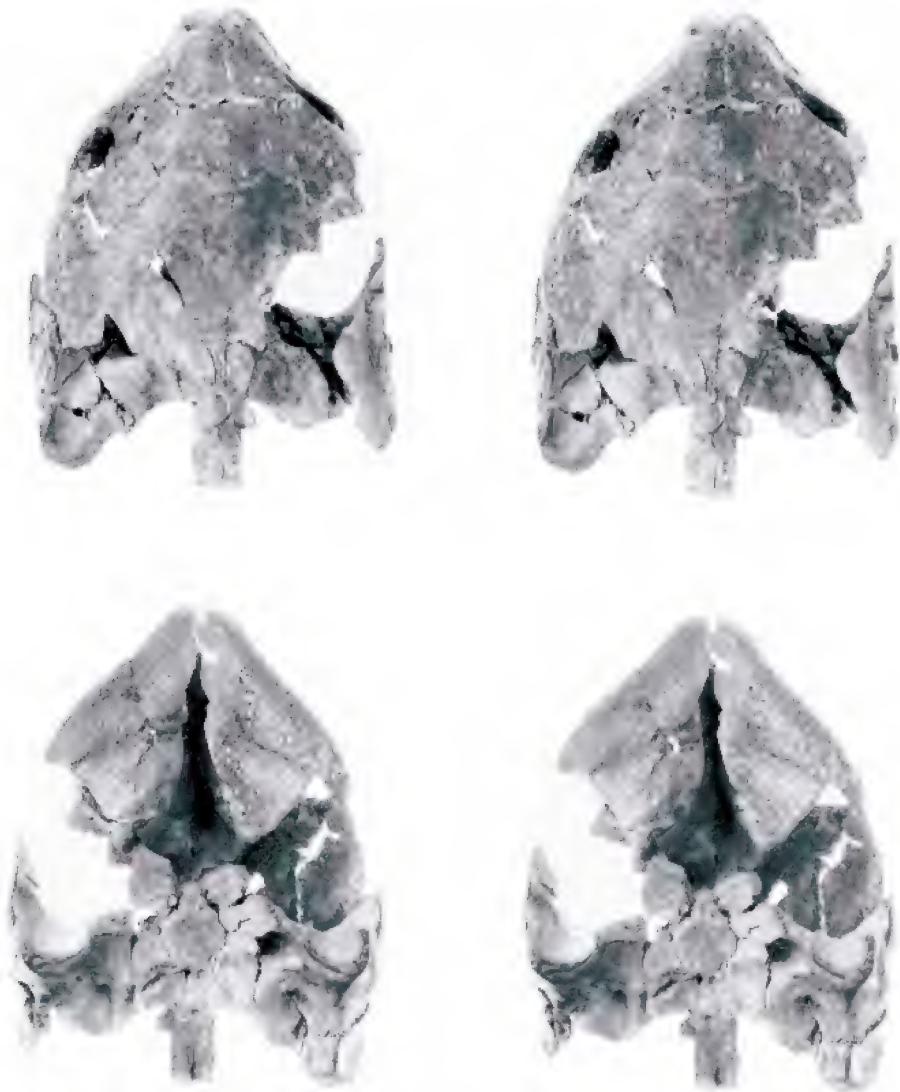


Fig. 12. *Bairdemys hartsteini*, new genus and species, AMNH 27222. Stereophotographs of dorsal (upper) and ventral (lower) views.

*mys venezuelensis*, “*Shweboemys*” *gaffneyi*, and “*Shweboemys*” *antiqua*, and were not separated on the midline as in *Shweboemys pilgrimi* and *Stereogenys*. Fragments of the processus trochlearis pterygoidei were found with AMNH 27222, but these do not have good contacts with the other pterygoid fragments that articulate with the rest of the skull. *Bairdemys venezuelensis*, however, shows a processus that extends laterally at right angles to the midline as in the other *Shweboemys* Group taxa and as in *Podocnemis expansa*.

A large, curved flange extends posteroventrally from the base of the processus trochlearis pterygoidei in the Podocnemididae. The flange is a posteroventral continuation of the sulcus palatinoptyergoideus. This flange is very thin and rarely preserved in fossils and is often broken in recent skulls. The posterior extent of this flange can be seen on the left side of AMNH 27222 and it is preserved in its entirety in *Bairdemys venezuelensis* MCZ 9417. It is a relatively large structure in *Bairdemys*, curving ventrally more than any other part of the skull. It forms the floor



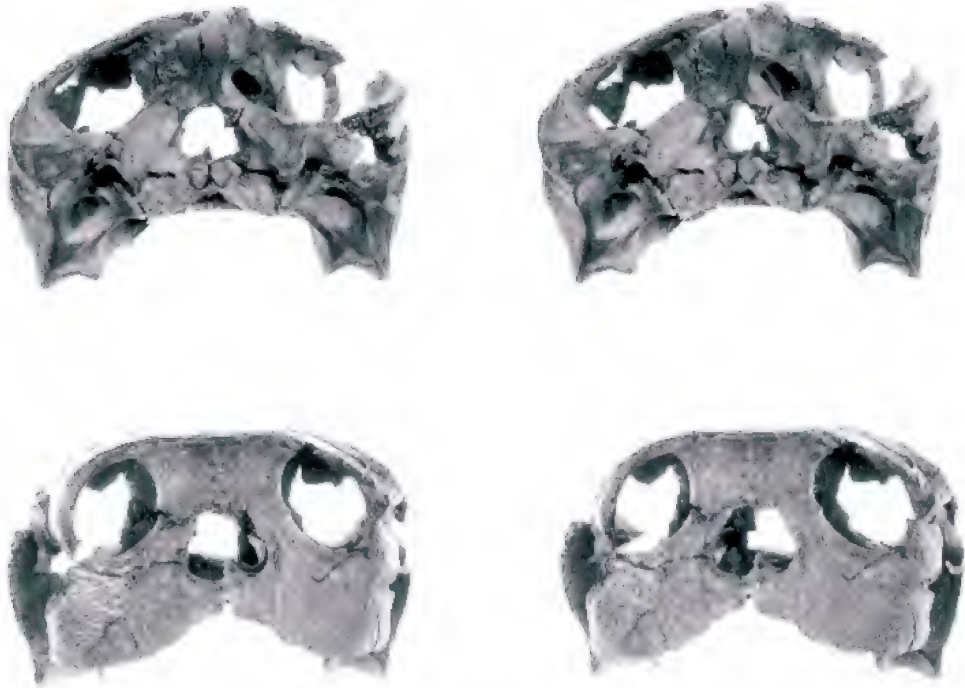


Fig. 13. *Bairdemys hartsteini*, new genus and species, AMNH 27222. Stereophotographs of posterior (upper) and anterior (lower) views.

and the posteroventral margin of the large cavum pterygoideus. The pterygoid contacts the basisphenoid along the base of the flange, allowing a ribbon of basisphenoid to be exposed in the wall of the cavum pterygoideus.

Posterolaterally the pterygoid reaches the pterygoid ramus of the quadrate. This contact is lateral to the cavum pterygoideus, which is formed by the pterygoid medially, ventrally, and laterally. The dorsal surface of the right pterygoid in *Bairdemys hartsteini* shows that the cavum extends anteromedially into the cavum cranii.

#### SUPRAOCCIPITAL

Most of the supraoccipital is present in *Bairdemys hartsteini*, but an indeterminate amount of the posterior end of the crista supraoccipitalis is missing. The supraoccipital is not well preserved or complete in any of the *Bairdemys venezuelensis* skulls. The anterior portion is present but variably crushed in all four skulls; it is best seen in MCZ 9417 and MCZ 9418. The crista supraoccipitalis is broken distally in all four skulls, but MCNC-

Pal-0002 has most of it preserved and is the only one with part of the horizontal plate present.

The supraoccipital in *Bairdemys* is very similar to other Podocnemididae anteriorly in the cavum cranii area, but does differ posteriorly. The supraoccipital in *Bairdemys hartsteini* lies under the parietals dorsally, but the exact position of the contact is ambiguous because of some wear on the sutural surfaces. The anteroventrolateral margins are broken, but the prootic contact is present on the right side. Posteroventrolaterally the supraoccipital contacts the opisthotic; the supraoccipital does not participate in the foramen stapedio-temporale or the canalis stapedio-temporalis. As in all other turtles the supraoccipital forms the recessus labyrinthicus supraoccipitalis and its associated anterior and posterior semicircular canals. Both canals are formed entirely by bone in AMNH 27222. The supraoccipital forms the dorsal margin of the foramen magnum and contacts the exoccipitals in a short suture at the edge of the foramen, as in other pelomedusids. Al-

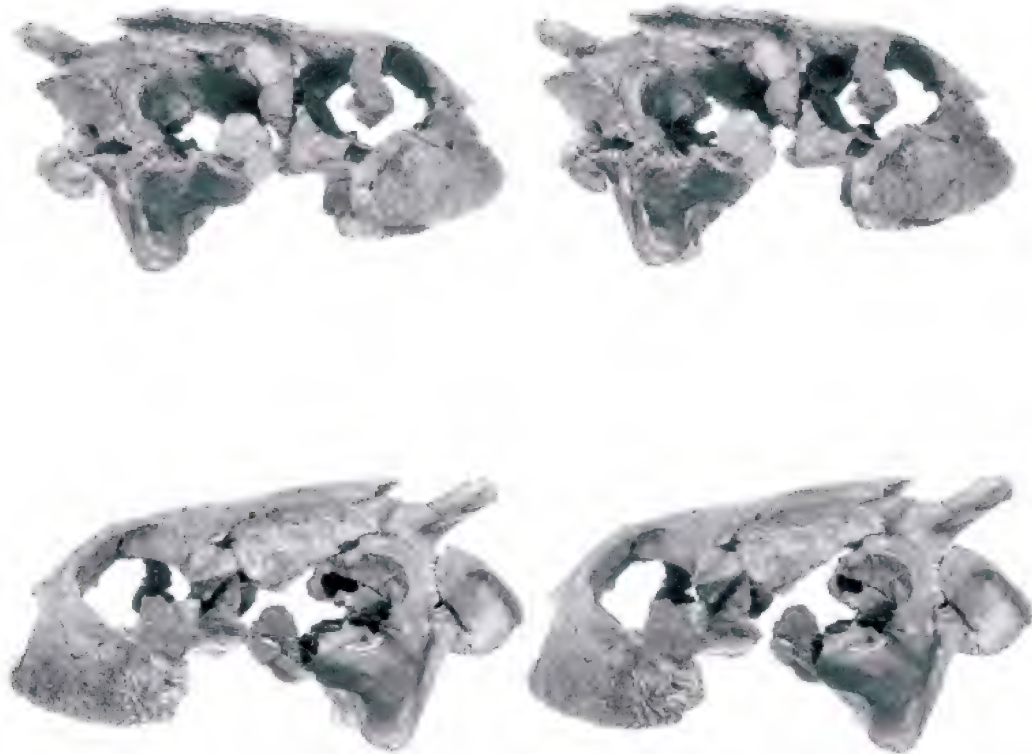


Fig. 14. *Bairdemys hartsteini*, new genus and species, AMNH 27222. Stereophotographs of right lateral (upper) and left lateral (lower) views.

though present in *Bairdemys venezuelensis*, the internal parts of the supraoccipital are not visible.

The posterior extension of the supraoccipital is the crista supraoccipitalis. In *Peltecephalus*, *Erymnochelys*, and most Podocnemididae outside the *Shweboemys* Group the crista is a vertical sheet, thickened ventrally to a varying degree. Some *Podocnemis* have a small, horizontal sheet of bone along the ventral edge of the crista; but in *Bairdemys* and "*Shweboemys*" *antiqua*, the horizontal part of the crista is very large and about as wide as the vertical sheet is high. In neither taxon is the crista complete, so the extent of the horizontal and vertical sheets is not known. The presence or absence of the horizontal sheet is not determinable in the other *Shweboemys* Group taxa.

#### EXOCCIPITAL

Both exoccipitals are present in *Bairdemys hartsteini*. The exoccipital is present in all

four *Bairdemys venezuelensis* skulls, but is best preserved in MCZ 9417 and MCZ 9418.

The exoccipital in *Bairdemys* forms most of the foramen magnum, meeting the supraoccipital dorsally, which prevents midline contact of the exoccipitals. Anterodorsally the exoccipital lies against the opisthotic. Ventrally the exoccipital contacts the basi-sphenoid. The exoccipitals meet on the midline in the foramen magnum and extend posteriorly, forming the neck of the condylus occipitalis. Both exoccipitals and the basioccipital form the condylus occipitalis.

Within the cavum cranii of *Bairdemys*, anterior to the foramen magnum, the exoccipital forms two foramina nervi hypoglossi. These penetrate posterolaterally through the exoccipital and combine to exit as one foramen between the condylus occipitalis and the foramen jugulare posterius. The single hypoglossal foramen is a *Shweboemys* Group synapomorphy. In most Pelomedusoides, as in most turtles, the hypoglossal nerves exit in two or three foramina.



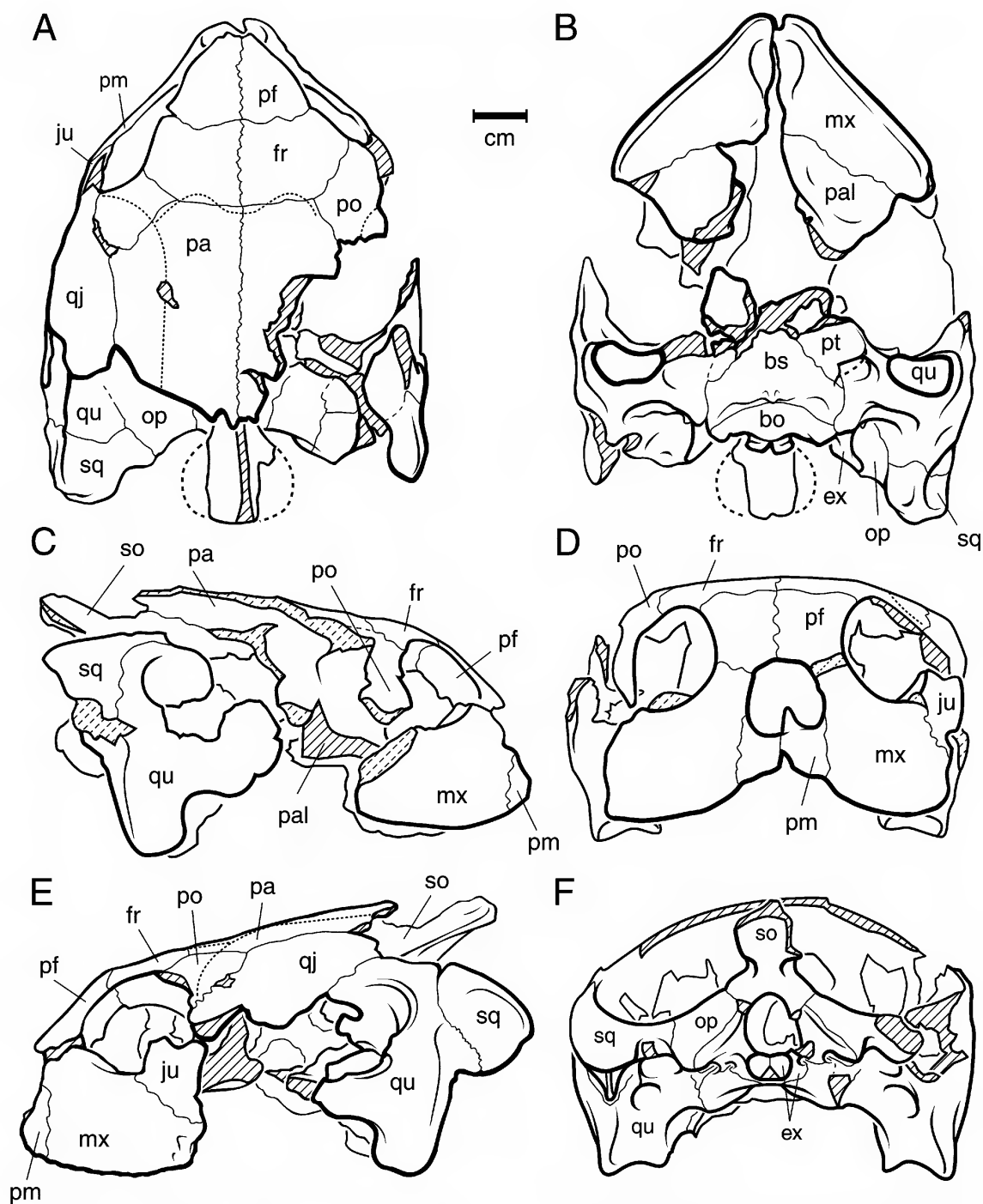


Fig. 15. *Bairdemys hartsteini*, new genus and species, AMNH 27222. A, dorsal; B, ventral; C, right lateral; D, anterior; E, left lateral; F, posterior. Key to figures 12 to 14.

The exoccipital also forms the posterior margin of the foramen jugulare anterius as in other turtles. The dorsal edge of the foramen jugulare anterius has a groove, presumably indicating the position of nerves X and XI, which also exit with the vena cerebialis posterior via the foramen jugulare anterius and foramen jugulare posterius. The more posterior of the internal foramina nervi hypoglossi has a small part of the basioccipital entering the margin. The basioccipital also enters the ventral margin of the foramen jugulare posterius.

#### BASIOCCIPITAL

All of the basioccipital is preserved in *Bairdemys hartsteini* except the posterior-most portion forming the surface of the condylus occipitalis. However, the size and shape of the missing basioccipital fragment can be determined from the sutural surfaces on the exoccipitals. The basioccipital of *Bairdemys venezuelensis* is preserved in all four skulls, but is best preserved in MCZ 9417 and MCNC-Pal-0001.

The basioccipital in *Bairdemys* is a broad, triangular element contacting the exoccipitals dorsally, the quadrates ventrolaterally, and the opisthotics dorsolaterally. Anteriorly there is a long, curved suture with the basisphenoid. The basioccipital forms part of the floor of the cavum labyrinthicum and a small part of the foramen jugulare anterius and foramen jugulare posterius. A tuberculum basioccipitale is formed entirely by the basioccipital and is less developed than in *Podocnemis expansa*. The basioccipital-basisphenoid suture in *Bairdemys* is curved convex anteriorly and roughly corresponds with the edge of a shallow indentation formed by the basioccipital.

#### PROOTIC

Only a small fragment of the right prootic containing the cavum labyrinthicum and recessus labyrinthicus prooticus is preserved in *Bairdemys hartsteini*. The prootic of *Bairdemys venezuelensis* is preserved in all four skulls, but it is not well preserved in any. The left prootic of MCZ 9417, right prootic of MCNC-Pal-0001, and the right prootic of MCZ 9418 are the better preserved and more

visible of the preserved bones. In MCNC-Pal-0002 the prootic is either not visible (right) or missing (left).

As in other Pelomedusoides the contacts of the prootic in *Bairdemys* are anterodorsally with the parietal, posterodorsally with the supraoccipital, posteriorly with the opisthotic, laterally with the quadrate, anteriorly and ventrally with the pterygoid, and ventromedially with the basisphenoid. Laterally the prootic forms the medial half of the foramen stapedio-temporale. The foramen in *Bairdemys* is slightly more anteriorly placed than in *Podocnemis*. The prootic has a groove for the stapelial artery extending onto its dorsal surface. The prootic in *Bairdemys* forms the posterior margin of the foramen nervi trigemini. The parietal forms the dorsal and anterodorsal margin and the pterygoid the ventral and anteroventral margin. The foramen is about the same size and shape in *Bairdemys* and in *Podocnemis*.

#### OPISTHOTIC

Both right and left opisthotics are complete in *Bairdemys hartsteini*, except for some breakage ventrally in the right opisthotic and along some of the margins. The opisthotic of *Bairdemys venezuelensis* is present, although damaged, on both sides of MCZ 9417 and MCNC-Pal-0001. In MCNC-Pal-0002 only fragments are present, and in MCZ 9418 the bone is badly crushed or hidden by matrix. The only clear sutures are in MCZ 9417.

The opisthotic contacts the supraoccipital dorsomedially, the prootic anterodorsally, the quadrate laterally and ventrolaterally, the squamosal posterodorsolaterally, the exoccipital posteromedially, and the basioccipital posteromedially and ventrally. As seen in *Bairdemys hartsteini* the opisthotic forms the recessus labyrinthicus opisthoticus and its associated semicircular canals. It also forms the posterior and dorsal walls of the cavum labyrinthicum and the anterior margin of the foramen jugulare anterius. Laterally the opisthotic roofs the cavum acustico-jugulare and forms part of the fenestra ovalis. Posteriorly the processus paroccipitalis is relatively short in *Bairdemys*, in contrast to the longer processus in *Podocnemis*.



## BASISPHENOID

Much of the basisphenoid in *Bairdemys hartsteini* is present, but is lacking the anterior rostrum basisphenoidale, and its dorsal surface is damaged and missing structures. The basisphenoid of *Bairdemys venezuelensis* is present and well preserved in MCZ 9417, somewhat damaged in MCZ 9418 and MCNC-Pal-0002, and heavily damaged in MCNC-Pal-0001; only its ventral surface is visible.

The basisphenoid is a triangular element with the pterygoids being separated by it anteriorly to a variable extent. Laterally the basisphenoid contacts the quadrate, and it has a long transverse suture with the basioccipital posteriorly. The basisphenoid in *Bairdemys* forms the medial part of the cavum pterygoideus and this can be seen to extend anteromedially between the basisphenoid and pterygoid. Most of the cavum is missing dorsally in AMNH 27222, but enough is preserved on the right side to determine its anterior extent. The cavum pterygoideus in *Bairdemys* is more extensive than in many other Podocnemididae, because the enlarged cavum extends into the sulcus cavernosus and erodes part of the wall. A section of the short canalis caroticus internus is preserved on the right side in *Bairdemys hartsteini*, but not on the left, and the foramen arterius canalis carotici interni is gone on both sides. The sella turcica, dorsum sellae, and rostrum basisphenoidale are not preserved in *Bairdemys hartsteini*, but part of the dorsal surface of the basisphenoid is present anterior to the basioccipital suture.

## RELATIONSHIPS

*Bairdemys* has the large cavum pterygoideus or "enlarged carotid chamber" synapomorphic of the Podocnemididae. It has a secondary palate formed by the maxilla and palatine with a narrow midline cleft found in *Shweboemys pilgrimi*, *Stereogenys cromeri*, "*Shweboemys*" *gaffneyi*, and "*Shweboemys*" *antiqua*. *Bairdemys* and these taxa are also united by an absent or very small foramen palatinum posterius and a very large contribution of the palatine to the triturating surface. Within this *Shweboemys* Group, *Bairdemys* has a triturating surface convexity

and a high and narrow labial ridge, both features shared with "*Shweboemys*" *antiqua*. A more rigorous assessment of *Bairdemys* and *Shweboemys* Group relationships awaits description of the other included taxa.

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## REFERENCES

- Albrecht, P. W. 1967. The cranial arteries and cranial arterial foramina of the turtle genera *Chrysemys*, *Sternotherus*, and *Trionyx*: a comparative study with analysis of possible evolutionary implications. *Tulane Studies in Zoology* 14(3): 81–99.
- Albrecht, P. W. 1976. The cranial arteries of turtles and their evolutionary significance. *Journal of Morphology* 149: 159–182.
- Andrews, C. W. 1901. Preliminary note on some recently discovered extinct vertebrates from Egypt (Part II). *Geological Magazine*, n.ser. Dec. IV, 8: 436–444.
- Andrews, C. W. 1903. On some Pleurodiran chelonians from the Eocene of the Fayum, Egypt. *Annals and Magazine of Natural History*, ser. 7, 11: 115–122.
- Andrews, C. W. 1906. A descriptive Catalog of the Tertiary Vertebrata of the Fayum, Egypt: I–XXXVII, London: Trustees British Museum (Natural History), 324 Pp.
- Antunes, M. T., and F. de Broin. 1988. Le Crétacé terminal de Beira Litoral, Portugal: remarques stratigraphiques et écologiques, étude complémentaire de *Rosasia soutoi* (Chelonii, Bothremydidae). *Ciências Terra* 9: 153–200.
- Bocquentin Villanueva, J. 1984. Un nuevo nettosuchidae (Crocodylia, Eusuchia) proveniente de la formación Urumaco (Mioceno Superior), Venezuela. *Ameghiniana* 21: 3–8.
- Bocquentin Villanueva, J., and E. Buffetaut. 1981. *Hesperogavialis cruxenti* N. Gen., N. Sp., Nouveau Gavialide (Crocodylia, Eusuchia) du Miocene Superieur (Huayquerien) D'Urumaco (Venezuela). *Géobios* 14(3): 415–419.
- Broin, F. de. 1988. Les tortues et le Gondwana. Examen des rapports entre le fractionnement du Gondwana au Crétacé et la dispersion géographique des tortues pleurodires à partir du Crétacé. *Studies in Palaeocheloniology* 2(5): 103–142.
- Cope, E. D. 1864. On the Limits and Relations of the Raniformes. *Proceedings of the Academy of Natural Sciences Philadelphia* 16: 181–183.
- Cope, E. D. 1868a. An examination of the Reptilia and Batrachia obtained by the Orton expedition to Equador (sic) and the upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences Philadelphia* 20: 96–140.
- Cope, E. D. 1868b. On the origin of genera. *Proceedings of the Academy of Natural Sciences Philadelphia* 20: 242–300.
- Díaz de Gamero, M. L. 1996. The changing course of the Orinoco River during the Neogene: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123: 385–402.
- Díaz de Gamero, M. L., and O. J. Linares. 1989. Estratigrafía y paleontología de la Formación Urumaco, del Mioceno-Tardío de Falcon Noroccidental. *Memorias VIII Congreso de Geología* 1: 419–438.
- Gaffney, E. S. 1979. Comparative cranial morphology of recent and fossil turtles. *Bulletin of the American Museum of Natural History* 164(2): 65–376.
- Gaffney, E. S., and P. A. Meylan. 1988. A phylogeny of turtles. In M. J. Benton (editor), *The phylogeny and classification of the tetrapods. Vol. 1, Amphibians, reptiles, birds. Syst. Assoc. Spec. Vol. 35A*: 157–219.
- Gaffney, E. S., K. E. Campbell, and R. C. Wood. 1998. Pelomedusoid Side-Necked Turtles from Late Miocene Sediments in Southwestern Amazonia. *American Museum Novitates* 3245: 1–12.
- Gaffney, E. S., D. de Almeida Campos, and R. Hirayama. 2001. *Cearachelys*, a New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Early Cretaceous of Brazil. *American Museum Novitates* 3319: 1–20.
- Iturralde-Vinent, M., and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* 238: 1–95.
- Jain, S. L. 1977. A new fossil pelomedusid turtle from the Upper Cretaceous Pisdura sediments, central India. *Journal of the Paleontological Society India* 20: 360–365.
- Jain, S. L. 1986. New pelomedusid turtle (Pleurodira: Chelonia) remains from Lameta Formation (Maastrichtian) at Dongargaon, central India, and a review of pelomedusids from India. *Journal of the Paleontological Society India* 31: 63–75.
- Kay, R. F., and R. H. Madden. 1997. Paleogeography and paleoecology. In R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (editors), *Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia*. Washington DC: Smithsonian Institution Press, 592 pp.
- Lapparent de Broin, F. de, and C. Werner. 1998. New late Cretaceous turtles from the western desert, Egypt. *Annales de Paléontologie* 84(2): 131–214.

- Linares, O. J. 1990. Mamíferos del Mioceno Medio-Tardío de Urumaco, Venezuela: Implicaciones paleobiogeográficas. Resúmenes de la Reunión conjunta de la Sociedad para el Estudio de los Mamíferos (SAREM) y la American Society of Mammalogists (ASM). Buenos Aires.
- Linnaeus, C. 1758. *Systema naturae*. 10th ed., vol. 1. Stockholm, 824 pp.
- Lundberg, J. G., O. J. Linares, M. E. Antonio, and P. Nass. 1988. *Phractocephalus hemiliop-terus* (Pimelodidae, Siluriformes) from the upper Miocene Urumaco Formation, Venezuela: a further case of evolutionary stasis and local extinction among South American fishes. *Journal of Vertebrate Paleontology* 8: 131–138.
- MacPhee, R. D. E., and A. R. Wyss. 1990. Oligo-Miocene vertebrates from Puerto Rico, with a catalog of localities. *American Museum Novitates* 2965: 1–45.
- Medina, C. J. 1976. Crocodilians from the later Tertiary of northwestern Venezuela. *Melan-oschus fisheri* sp. nov. *Breviora* 438: 1–14.
- Meylan, P. A. 1996. Skeletal morphology and relationships of the Early Cretaceous side-necked turtle, *Araripemys barreto* (Testudines: Pelomedusoides: Araripemydidae), from the Santana Formation of Brazil. *Journal of Vertebrate Paleontology* 16(1): 20–33.
- Pascual, R., and M. L. Díaz de Gamero. 1969. Sobre la presencia del genero *Eumegamys* (Rodentia, Caviomorpha) en la formación Urumaco del Estado Falcón (Venezuela). Su significación cronológica. *Association Venezolana Geol. Bol. Inf., Min. Pet.* 12(10): 369–387.
- Reinach, A. von. 1903. Schildkrötenreste aus dem ägyptischen Tertiär. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 29(1): 1–64.
- Sánchez-Villagra, M. R., O. J. Linares, and A. Paolillo. 1995. Consideraciones sobre la sistematización de las tortugas del género *Chelus* (Pleurodira: Chelidae) y nuevas evidencias fósiles del Mioceno de Colombia y Venezuela. *Ameghiniana* 32(2): 159–167.
- Sánchez-Villagra, M. R., R. J. Burnham, D. C. Campbell, R. M. Feldmann, E. S. Gaffney, R. F. Kay, R. Lozsán, R. Purdy, and J.G.M. Thewissen. 2000. A new near-shore marine fauna and flora from the Early Neogene of Northwestern Venezuela. *Journal of Paleontology* 74(5): 957–968.
- Schumacher, G.-H. 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodilians. In C. Gans, and T.S. Parsons (editors), *Biology of the Reptilia*, Vol. 4: 101–199.
- Swinton, W. E. 1939. A new fossil fresh-water tortoise from Burma. *Records of the Geological Survey of India* 74(4): 548–551.
- Williams, E. E. 1954a. A key and description of the living species of the genus *Podocnemis* (sensu Boulenger), Testudines, Pelomedusidae. *Bulletin of the Museum of Comparative Zoology* 111: 277–295.
- Wood, R. C. 1970. A review of the fossil Pelomedusidae (Testudines, Pleurodira) of Asia. *Breviora* 357: 1–24.
- Wood, R. C. 1976a. *Stupendemys geographicus*, the world's largest turtle. *Breviora* 436: 1–31.
- Wood, R. C. 1976b. Two new species of *Chelus* (Testudines: Pleurodira) from the Late Tertiary of northern South America. *Breviora* 435: 1–26.
- Wood, R. C., and M. L. Díaz de Gamero. 1971. *Podocnemis venezuelensis*, a new fossil pelomedusid (Testudines, Pleurodira) from the Pliocene of Venezuela and a review of the history of *Podocnemis* in South America. *Breviora* 376: 1–23.
- Wood, R. C., and B. Patterson. 1973. A fossil trionychid turtle from South America. *Breviora* 405: 1–10.

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